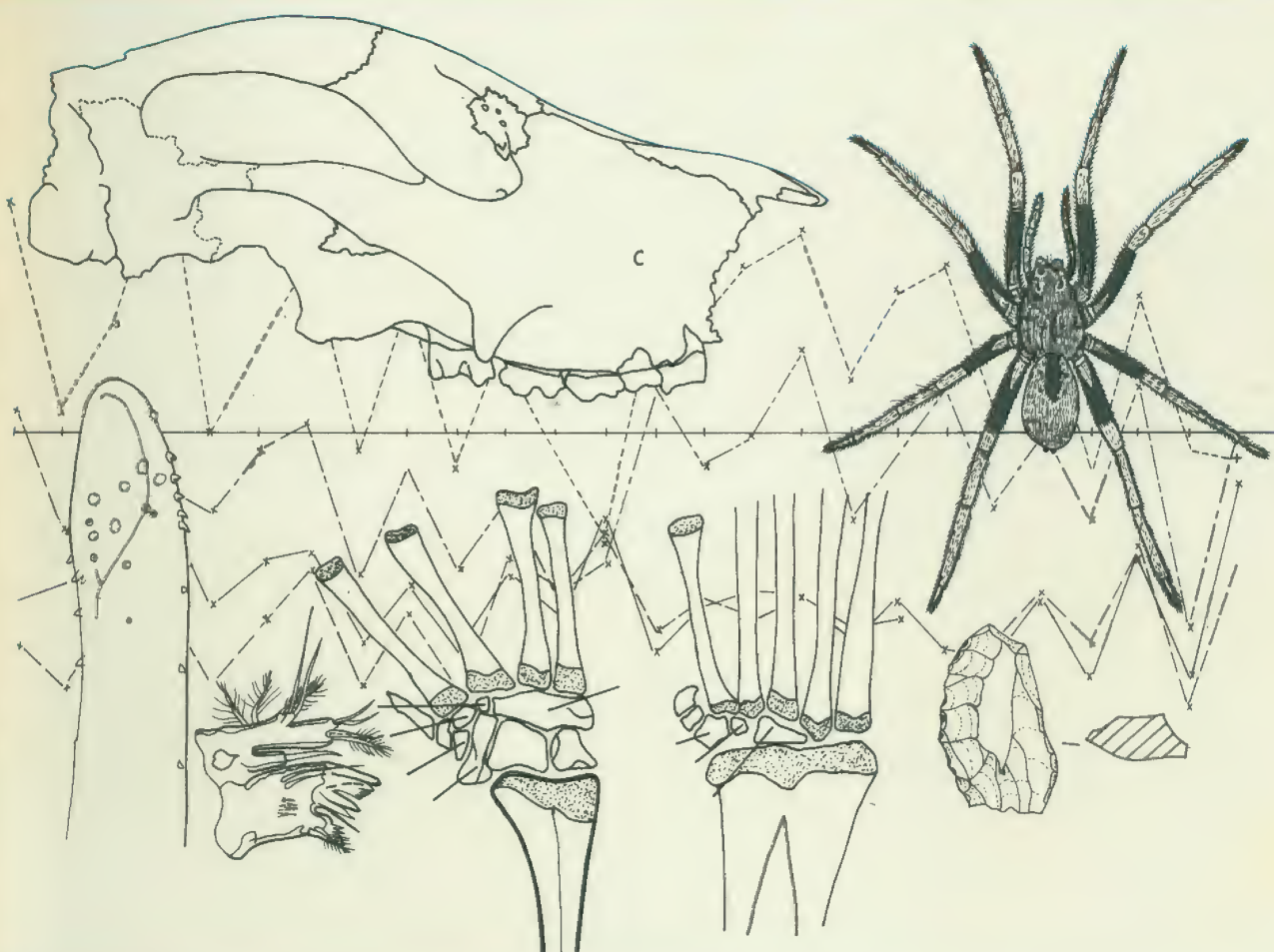


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THE GENUS *PROTEMNODON* OWEN (MARSUPIALIA: MACROPODIDAE)
IN THE UPPER CAINOZOIC DEPOSITS OF QUEENSLAND

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ABSTRACT

The genus *Protemnodon* Owen, 1874, is re-defined on the basis of extensive collections in the Queensland Museum, derived largely from the Upper Cainozoic fluviatile deposits of the Darling Downs area, southeastern Queensland. Five species of this extinct macropodid genus are recognized, three of which, *P. anak*, *P. brehus* and *P. roechus* are found to be restricted to Pleistocene sediments. Two new species, *P. chinchillaensis* and *P. devisi*, are described from the Late Pliocene Chinchilla Sand in the western Darling Downs and of these, *P. chinchillaensis* is at present known only from that Formation. *P. devisi* is shown to be present also in unnamed sediments near Mullaley, New South Wales. It is morphologically very similar and probably closely related to *P. otibandus*, described from the Middle Pliocene Otibanda Formation in New Guinea and reported from the Lower Pliocene marine Jemmy's Point Formation in Victoria. Both new species are shown to represent major elements in the Chinchilla fauna.

Samples in all species defined are sufficiently large to enable statistical evaluation of most of the cheek teeth to be undertaken and results are generally in keeping with what has been recorded for other fossil and living macropodid populations.

Remains of macropodids comprise a major part of the collections of fossil marsupials derived from the Upper Cainozoic deposits of Queensland, and among these, the genus *Protemnodon* Owen, 1874, is particularly well represented. By far the majority of specimens referable to this genus in the holdings of the Queensland Museum have been derived from the classical Darling Downs deposits in southeastern Queensland. These form the basis for the present study.

The presence of fossil marsupials was noted in the Darling Downs area shortly after the first settlement of the area in the early 1840's. Early collections appear to have been restricted to material derived from high terrace Pleistocene fluviatile deposits along the Condamine River and its major tributaries in the eastern portion of the district. Later collections also accumulated from the Chinchilla area in the western Darling Downs and for many years specimens from both these sources were ascribed a Pleistocene age. It has now been shown by Bartholomai (1972a) that an age difference exists between the deposits. The Chinchilla Sand in the west is considered to be of Late Pliocene age. The probability of this age difference existing had been originally suggested by Woods (1956)

and prior to evidence for superposition becoming available, was strongly supported by the presence between them of faunal distinctions, usually at a specific level.

A number of studies on extinct macropodids occurring in the Darling Downs deposits have already been presented (Woods, 1960; Bartholomai, 1963, 1966, 1967, 1970, 1972a, 1972b) and the present study constitutes a contribution to a better understanding of the taxonomy of the genus *Protemnodon* in the light of the large samples available and the improved knowledge of the geological history of the area. The *Protemnodon* samples, because of their size, allow a reassessment of the species represented, involving an evaluation of the teeth, and other parameters and morphological variation present. Results are of potential value in correlation of Australian continental deposits and in providing a better basis towards an understanding of the Upper Cainozoic evolutionary history of this interesting genus.

The Queensland study of *Protemnodon* is supported by a less detailed investigation of the distribution of the genus in Australia based on collections in Australian museums, and on published work. Results, particularly from the available holdings of the Australian Museum, Sydney, are of value in consideration of the eastern Australian distribution of *Protemnodon* and the geographical variation present. Exact temporal relationships of these samples are, however, difficult to determine. Specimens from the Australian Museum are prefixed throughout by AM.

All measurements throughout are in millimetres.

Genus *Protemnodon* Owen, 1874

Protemnodon Owen, 1873, p. 128 (*nomen nudum*).

Protemnodon Owen, 1874, pp. 274–5 (type species *Protemnodon anak* Owen, 1874, by subsequent designation of Simpson, 1930, and restated by Tate and Archbold, 1937, = *Macropus anak* Owen, 1859, *nomen nudum*). Palmer (1904) had previously questionably suggested *P. anak* as the type species.

Considerable confusion exists regarding the taxonomic status of the genus *Protemnodon* Owen, based on fossil material, and on the genera *Macropus* Shaw, 1790, and *Wallabia* Trouessart, 1905, based on modern species (Ride, 1962).

Stirton (1963) provides a very full discussion on previous concepts of *Protemnodon* and attempts, through an extended comparison of cranial and dental characters, to justify its separation from other macropodines. Unfortunately, his revised generic diagnosis for *Protemnodon*, includes many characters common to most macropodine genera. Stirton (1963) emphasises, however, that the separation of *Protemnodon* must depend upon utilization of all available criteria and cannot be effected by single character considerations. He concludes that the genus is separable from *Wallabia sensu lato* (Calaby, 1966) and from other macropodine genera and this contention is supported by the present study, but Stirton's limits for the genus *Wallabia* are not supported by either recent or fossil taxonomic considerations (Bartholomai, 1972a). Previously, Raven (1929), followed by many subsequent authorities, had considered *Wallabia* and *Protemnodon* synonymous, although Troughton (1957) reiterated their generic distinctness but presented little evidence to support this conclusion. Stirton (1963) has evaluated some

of the characters used by Tate (1948) who supported their synonymy and has indicated the extreme difficulty of defining generic limits, a result of the marked convergence in the evolution of the subfamily as a whole (Bartholomai, 1972a).

The confusion initiated by Owen (1877) regarding the association of upper teeth of *Protemnodon* with the named mandibular remains, and the association of upper and lower dentigenous fragments of the genus *Sthenurus* Owen, 1874, has also been outlined by Stirton (1963). Owen's misidentifications have been shown to have resulted from the misconception that the genera were closely related, and were aided by the sequence of discovery of the various remains.

No doubt currently exists regarding the correct association of fragments in *Protemnodon*, although much confusion remains regarding the identity and number of species present and the correct association of upper and lower jaw fragments within these.

Owen (1874) described four species of *Protemnodon* from the Queensland Pleistocene fluviatile deposits. These he named *P. anak*, *P. og*, *P. roechus* and *P. mimas*. In the same publication, Owen (1874) also described *Sthenurus brehus* (= *P. brehus*) from the Pleistocene cave earth deposits at Wellington Caves, New South Wales. An additional Pleistocene species, *P. antaeus* was later described by Owen (1877) from the fluviatile deposits of the eastern Darling Downs. All species were based on mandibular remains, with the exception of *P. brehus*.

Lydekker (1887) reduced the number of species recognized to three, *P. anak*, *P. brehus* and *P. roechus*, but referred them to the genus *Macropus*. The number was again reduced by De Vis (1895) and only one species, *P. anak*, was recognized at that time. De Vis employed the generic name *Halmaturus* Illiger, 1811, a junior secondary homonym of *Macropus*, for the species. Since that time there have been several suggestions that the variation exhibited in the Upper Cainozoic protemnodonts would justify the recognition of a larger number of species. Stirton (1963) states that even if only late Pleistocene fossils occur in the Darling Downs, it is not unreasonable that two species could be represented. He indicates that it is extremely doubtful that there are as many as six, and still questionable that there are more than two.

Fossiliferous late Pleistocene deposits at Lake Menindee, New South Wales, have been reported by Tedford (1967) who records *P. brehus* as a moderately rare element in the fauna. It is possible that this sample represents a mixture of two large species. Cranial and post-cranial remains have been described. Tedford (1967) suggests that De Vis's (1895) concepts on the morphological limits of Owen's species were very wide, and by accepting *P. brehus* as a valid species within the *Protemnodon* group, he infers that at least two species exist in the late Pleistocene deposits.

Two species, *P. otibandus* and *P. buloloensis* have been described by Plane (1967) from the Middle Pliocene Awe Fauna of the Otibanda Formation, New Guinea. Plane (1972) has recorded *P. buloloensis* in the marine Lower Pliocene (Kalimnan) Jemmy's Point Formation in Victoria and has suggested that this species is also present in the Chinchilla fauna. *P. buloloensis* shows some morphological similarities to part of the Chinchilla Sand sample but, although close relationships are apparent, sufficient differences exist for this to be maintained as a distinct mainland Pliocene species. It is of interest to note that elements of the post-cranial skeleton are also known for *Protemnodon* in the

Awe Fauna, including the peculiarly robust, short pes, and the forearm and manus in *P. otibandus*. No attempt has been made to sort the post-cranial elements of *Protemnodon* in the Queensland Museum holdings, although it is apparent that morphologically similar elements to those described from the Otibanda Formation are present in reasonably large numbers from both the Pleistocene and Late Pliocene deposits.

The present study indicates that five species of *Protemnodon* are represented in the Upper Cainozoic deposits of the Darling Downs. No taxonomic distinctions are evident to suggest additional taxa within samples collected from elsewhere in Queensland or used for comparison from New South Wales localities. Three of the species present are derived from the Pleistocene fluvial deposits and cave and fissure fill deposits of similar or perhaps younger age, while two species occur in the Chinchilla Sand. Nomenclature for the Pleistocene species follows that previously outlined by Lydekker (1887).

Representative histograms prepared for cheek teeth dimensions in the combined *Protemnodon* sample from the Pleistocene deposits, illustrated in Figure 1, show marked bimodality for the characters considered, and this is true for most parameters in the sample. A similar but less well-defined bimodality exists in the combined sample for the Chinchilla Sand material. Within the Pleistocene sample, the bimodality is by no means equal, there being considerably more specimens represented relating to lower values than to higher values in the characters assessed. Males and females in modern macropodine populations are represented approximately by nearly equal numbers of individuals (Kirkpatrick, pers. comm.). For this reason, the size differences which exist within the broad groups defined by the histograms suggest that these do not represent sexual dimorphism within single species. Bartholomai (1971) has shown that in the living Grey Kangaroo, *Macropus giganteus* Shaw, 1790, sexual dimorphism in the cheek teeth is a factor warranting attention but this does not manifest itself in spectacularly bimodal frequency distributions. In the same study, Bartholomai also indicates that in the large, living Sandy Wallaby, *M. agilis* (Gould, 1842), no significant sexual dimorphism is present in the sizes of the cheek teeth. In both living species mentioned, marked dimorphism does appear to exist in other characters less readily observed in fossil specimens and of these, for example, basicranial length appears to differ to a much greater extent between the sexes.

Bartholomai (1972a) suggests that the diversification of the fauna recorded from the Darling Downs deposits may reflect accumulations deposited under climatic fluctuations with attendant faunal shifts so that sympatric conditions of existence need not necessarily apply. It is inconceivable from comparison with extant species, however, that the differences in each combined Upper Cainozoic sample could represent subspecific differences within single species. Similarly, the differences within each combined sample cannot be attributed to successional subspeciation because material from both limits of a particular histogram is derived from the same stratigraphic level in single sites.

The size differences which occur in both the Pleistocene and Late Pliocene samples are regarded as being of taxonomic importance, and can be utilized in the initial sorting of collections. Together with some morphological characters, sufficient differences are available to establish the distinctness of the species here redefined and described. As an example, the individuals contributing to the larger values in the bimodal frequency

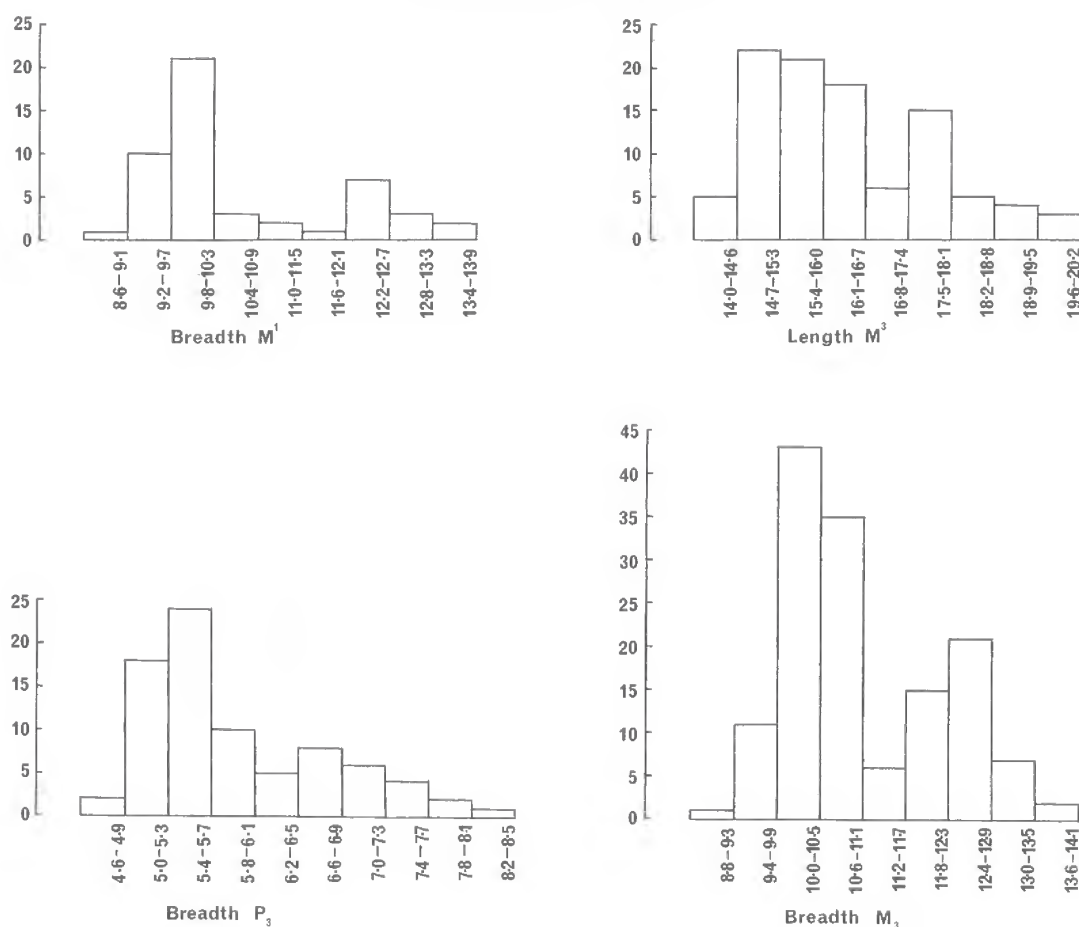


FIG. 1: Representative histograms for cheek teeth parameters in the combined *Protamnodon* samples from the Pleistocene fluviatile deposits of the eastern Darling Downs.

distributions for the Pleistocene material are further separable into two species, *P. brehus* and *P. roechus*, by structural differences, while those contributing to the smaller values differ morphologically from these, and are referable to *P. anak*. In no case, however, is complete separation of a population possible by size alone. It is obvious that, because of initial overlap of values, the statistical Coefficient of Difference would fall well below the value of 1.5 or larger, suggested by Ride (1964) to be required to define even subspecific differences. As with characters of value in defining the generic limits, it is necessary to apply as many criteria as possible in the separation of the species.

Cranial remains in all species, for the most part, are fragmentary. Fortunately exceptions to this are present, although apart from *P. anak* only one reasonably complete cranium is known in the Queensland collections. Within *P. anak* only F616, an almost

complete cranium, is present in an undistorted condition but this is adequately supported by several distorted specimens. *P. roechus* is represented by one partial cranium, F6581. A partial cranium of *P. brehus* is present in the Western Australian Museum, from Lake Tandau in the Lower Darling Region, New South Wales, but at present the Late Pliocene species lack referred complete or near complete crania. Knowledge of the cranial anatomy of these is restricted to fragmentary maxillary remains.

Stirton (1963, figs. 2–3) has illustrated partial crania, but of these only the subject of his figure 2, AM F2221, of *P. anak*, would appear to be referable with certainty to the genus. The second specimen illustrated by Stirton (1963, fig. 3), AM F16490, appears to differ markedly from crania of *P. anak* in the Queensland Museum and from the other specimen figured by Stirton (1963). The most obvious differences are seen in the posterior view, illustrated in Stirton (1963, fig. 3a), where the zygomatic processes of the squamosals are markedly convergent dorsally and nearly flattened laterally, whereas in *P. anak* these are less convergent dorsally and present a rounded lateral profile. The trend towards dorsal convergence in the cranium, AM F16490, is also seen in the occipital surface which is relatively narrower dorsally and broader ventrally, this imparting a moderate divergence to the paraoccipital processes. The cranium, F6581, here referred to *P. roechus*, does present greater dorsal convergence in posterior view than in *P. anak* and AM F16490 may relate to this or the other larger protemnodont, *P. brehus*. No cheek teeth are preserved in AM F16490 and thus some doubt remains regarding the taxonomic position of this specimen.

Stirton (1963) has attempted a reconstruction of the cranium of *Protemnodon* but has had to restore much of the dorsal outline. It is felt that the premaxillary and the upper incisors added to this reconstruction and based upon AM F37806, are referable to one of the larger species of *Protemnodon* from the Pleistocene, whereas the bulk of the recon-

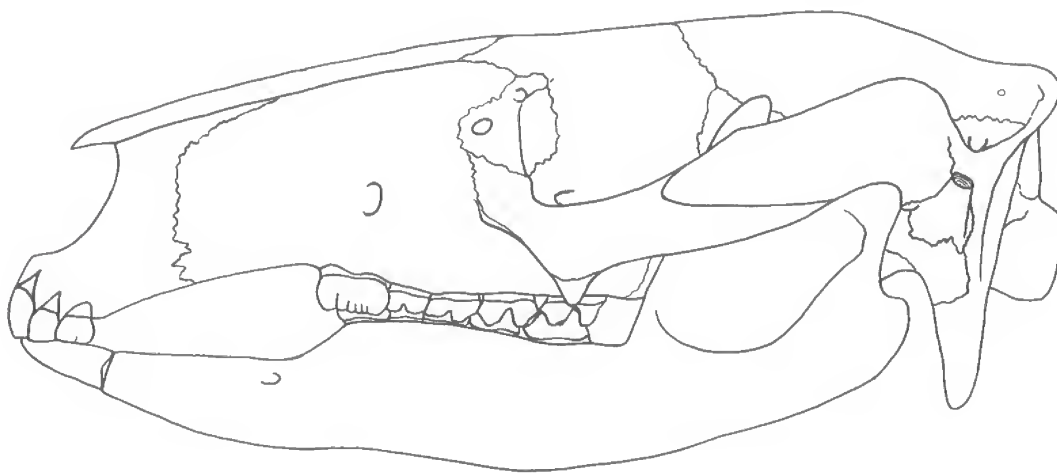


FIG. 2: Reconstruction of the cranium of *Protemnodon anak* Owen, based on the skull, F616, the premaxilla, F651, and the mandibular ramus, F617, $\times \frac{1}{2}$.

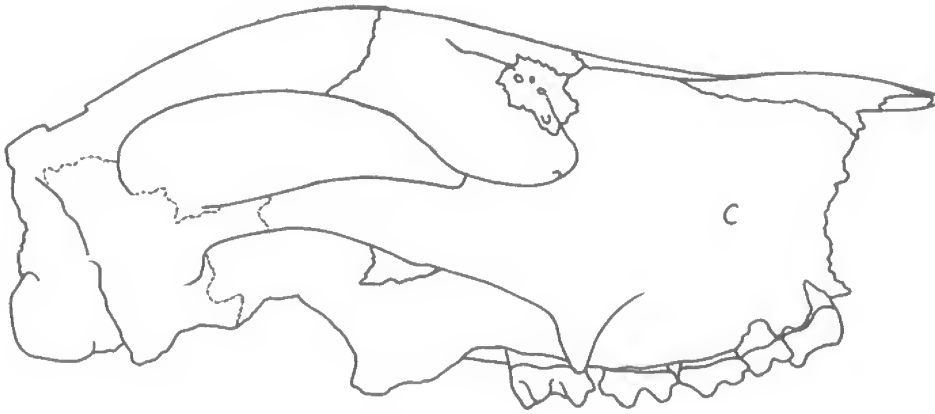


FIG. 3: Outline illustration of partial cranium, F6581, of *Protemnodon roechus* Owen, $\times \frac{1}{2}$.

struction is based on AM F2221, of *P. anak*. The reconstruction of the skull of the type species, *P. anak*, here presented in Figure 2, illustrates the much flatter nature of the dorsal surface of the cranium in that species compared with the genera *Macropus* Shaw and *Wallabia* Trouessart and with Stirton's (1963) reconstruction. An outline illustration of the cranium of *P. roechus* is presented in Figure 3, and illustrates the extent of some of the differences present between the larger and smaller Pleistocene *Protemnodon* species. The differences relate particularly to the length of the nasals but the shape of the premaxillae and the size of the upper incisors are also important. The specimen of *P. brehus* in the Western Australian Museum from Lake Tandau, although incomplete, suggests that shortening of the nasals may also be a feature of that species; this is supported by the specimen illustrated by Owen (1877, pl. 109, figs. 9–10).

Much has been written on the similarities and differences present between the crania of *Protemnodon* and other living and extinct macropodine genera (Stirton, 1963). A series of equal area grid diagrams, as proposed by Thompson (1959), have been prepared using a specimen of *Wallabia bicolor* (Desmarest, 1804), the type species of *Wallabia*, as a standard, and including specimens of *Protemnodon* and species of *Macropus* for comparison. To add some measure of control, all specimens compared are at a similar stage of dental eruption. Results are illustrated in Figure 4. These show that at least in the type species of *Protemnodon*, the cranium is more flattened, more elongate in the area of the diastema, broader across the anterior of the palate, and with the alveoli for the incisors forming a broader U-shaped pattern in occlusal view than in *W. bicolor*. The basisphenoid and presphenoid are more posteriorly positioned with respect to the posterior palatine margin. Some distortion precludes the use of the cranium of *P. roechus* in this regard, but because of restriction of the nasals, the grid distortion would indicate shortening of this area compared with both *W. bicolor* and *P. anak* and the same is also probably true of *P. brehus*.

Species of *Macropus* show great similarity in the degree of grid distortion produced and most pronounced differences relate only to relative size. Differences from *Wallabia*

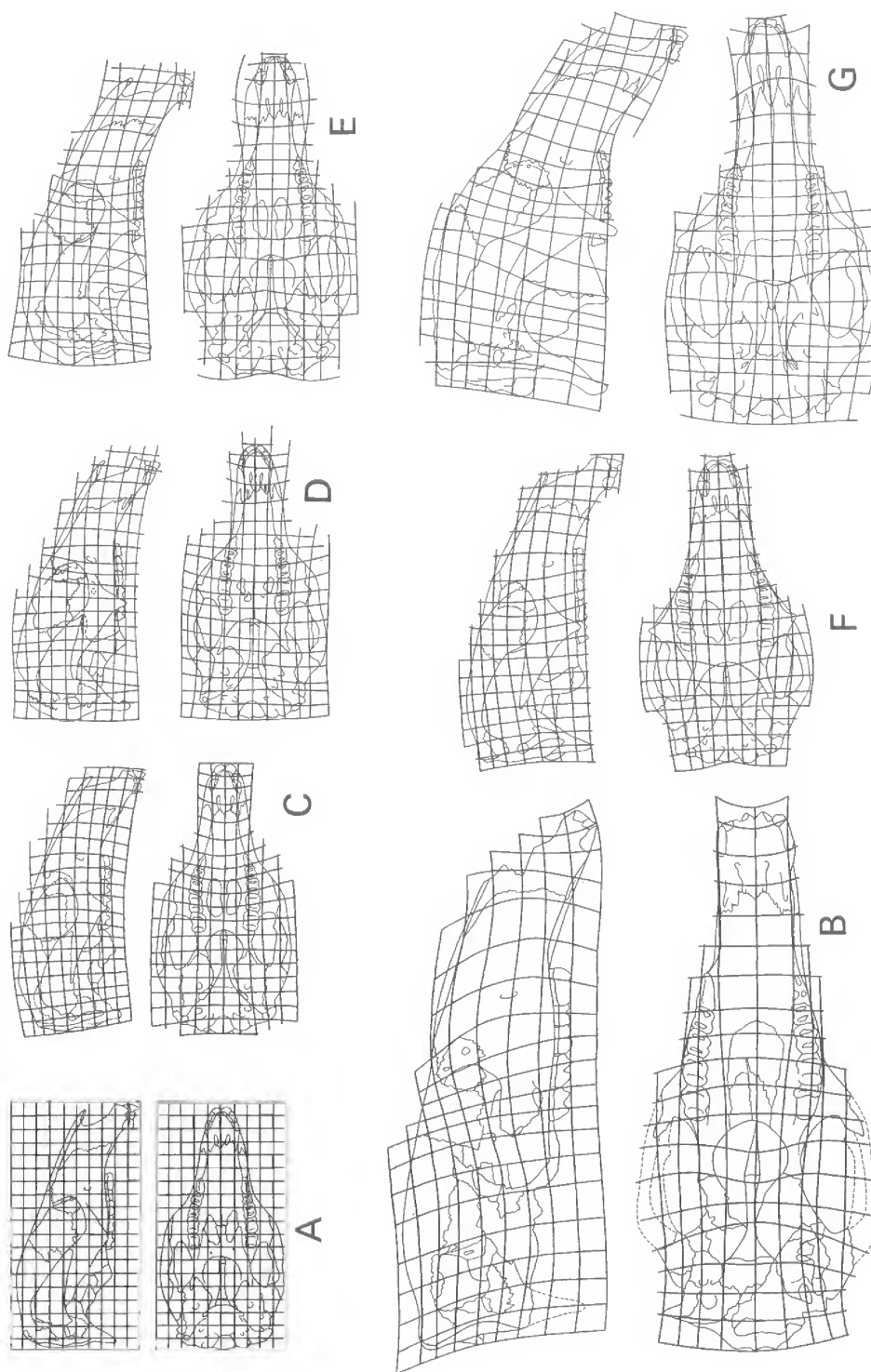


FIG. 4: Equal area grid diagrams based on A, *Wallabia bicolor* as standard, for B, *Protomnodon anak* (F616); C, *Macropus dorsalis*; D, *M. rufogrisea*; E, *M. elegans*; F, *M. agilis*; and G, *M. giganteus*.

and *Protemnodon* are considerable. The most obvious distinction lies in the much stronger declination of the rostral area of the skull, the elongation of this area, particularly anteriorly, and the shortening and broadening of the base of the cranium. Such diagrams, although representing generalizations by the nature of their preparation, are considered of value in illustrating and indicating differences in these morphologically similar genera.

Protemnodon is widespread in its distribution throughout Australia during the Pleistocene and is recorded from numerous localities in all States except the Northern Territory. Pliocene occurrences are less well represented in collections, but the genus is known from the Otibanda Formation in New Guinea, from the Chinchilla Sand in Queensland, and from the Lower Pliocene Jemmy's Point Formation (Plane, 1972) and possibly the late Pliocene Hamilton Fauna in Victoria (Turnbull and Lundelius, 1970). Earlier history of the group is not well documented although Stirton *et al.* (1967b) have recorded but not described a *protemnodont* from the Wipijiri Formation in the Lake Eyre Basin, South Australia. Bartholomai (1972a) has suggested that major radiation in *Protemnodon*, similar to other macropodids, probably took place in Australasia during and particularly after the Miocene.

REVISED GENERIC DIAGNOSIS: Cranium flattened with limited declination of rostral area, diastema elongate, and anterior of palate broad; high, thin lateroventral ovale crest separates pterygoid cavity from ovale foramen and continues onto alisphenoid bulla as posterior rim of foramen. Palatine vacuities absent. Upper incisors broadly U-shaped in occlusal view. Canine usually absent but may be present in vestigial state. P² elongate with high longitudinal crest and low cingulum; crest transected by two variable, vertical or near vertical sets of labial and lingual ridges with production of cuspules at crest. Posterior fossette present. DP³ molariform, similar to upper molars. P³ elongate with high longitudinal crest and low lingual cingulum which terminates above paracone or more anteriorly; crest transected by two to five sets of vertical or near vertical labial and lingual ridges, usually with development of cuspules at crest; hypocone prominent and posterior fossette well defined. Upper molars with forelink usually absent but strong anterior ridge from paracone to anterior cingulum usually present; median valley near planar transversely; accessory ridge from paracone to metacone usually crosses labial moiety of median valley.

Mandible with diastema long, and with well defined lateral groove extending posteriorly as far as M₃ in some species; symphysis elongate, unankylosed, varying in elevation from horizontal to about 20° to base of mandible; articular facet of condyle nearly twice as wide transversely as antero-posteriorly long. I₁ vertically deep, lanceolate, with tip strongly incurved. P₂ elongate, secant, with longitudinal crest straight or somewhat curved, and with crest transected by vertical or near vertical sets of labial and lingual ridges. DP₃ molariform, similar to lower molars; P₃ elongate, with longitudinal crest transected by one to five sets of vertical or near vertical labial and lingual ridges, with cuspules usually developed at crest; crest straight or somewhat curved. Lower molars with talonid basin narrowly U-shaped, with or without tuberculation at lingual extremity and near planar transversely; posterior cingulum may be present.

Protemnodon anak Owen, 1874

(Plates 9–12)

Macropus anak Owen, 1859, p. 185 (*nomen nudum*).*Protemnodon anak* Owen, 1873, p. 128 (*nomen nudum*).*Protemnodon og* Owen, 1873, p. 128 (*nomen nudum*).*Protemnodon anak* Owen, 1874, pp. 275–7, pl. 25, figs. 1–4, 7–10, 11–14; 1877, pp. 428–30, pl. 85, figs. 1–4, 7–10, 11–14; Etheridge Jnr., 1892, p. 677; Raven, 1929, p. 255; Simpson, 1930, p. 76; Tate and Archbold, 1937, p. 410; Tate, 1948, p. 297; Troughton, 1957, p. 187; Stirton, 1963, p. 137, fig. 13a.*Protemnodon og* Owen, 1874, pp. 277–8, pl. 25, figs. 5–6; 1877, p. 430, pl. 85, figs. 5–6; Etheridge Jnr., 1892, p. 678; Palmer, 1904, p. 883; Simpson, 1930, p. 76; Stirton, 1963, p. 139, fig. 13b.*Halmaturus anak* (Owen): Krefft, 1875, p. 208; De Vis, 1895 (*partim*), pp. 104–9, pl. 17, figs. 5–10.*Sthenurus atlas* Owen, 1876 (*partim*), pp. 210–2, pl. 25, fig. 2, pl. 26, fig. 4.*Macropus anak* (Owen): Flower, 1884, p. 715; Lydekker, 1887, pp. 214–8; Lydekker, 1894, p. 257; Lydekker, 1896, p. 257; Palmer, 1904, p. 883.[?] *Macropus anak* (Owen): Scott and Lord, 1924, pp. 6, 8.

MATERIAL: F3398, cast of holotype of *Protemnodon anak* Owen, British Museum (Natural History) No. M.1895, partial left mandibular ramus with P_3 – M_4 , adult, Darling Downs, (figd Owen, 1874, pl. 25, figs. 1–2; 1877, pl. 85, figs. 1–2).

F3396, cast of holotype of *Protemnodon og* Owen, British Museum (Natural History) No. 35963, partial left mandibular ramus with P_3 – M_4 , adult, Gowrie, Darling Downs, (figd Owen, 1874, pl. 25, figs. 5–6; 1877, pl. 85, figs. 5–6).

Seventy-two juvenile mandibular rami, 105 adult mandibular rami, 16 isolated lower teeth, 6 partial adult crania, 6 premaxillary remains, 19 juvenile maxillae, 71 adult maxillae and 26 isolated upper teeth from the following localities in the eastern Darling Downs: King Creek; King Creek, between Pilton and Nobby; King Creek, at Ravensthorpe, Upper Pilton; King Creek, near M.R. 039454 Clifton 1 mile map; King Creek, at M.R. 039454 Clifton 1 mile map; King Creek, at M.R. 134444 Liverpool Range 1 mile map; King Creek, at M.R. 098465 Liverpool Range 1 mile map; King Creek, at M.R. 873335 Clifton 1 mile map; King Creek, near M.R. 047452 Clifton 1 mile map; at M.R. 951360 Clifton 1 mile map; Ravensthorpe, Pilton; Clifton; Gowrie; Gowrie Creek; ? Gowrie; near Dalby; Jimbour, via Macalister; Jimbour Creek; Springvale, near St Ruth; Condamine River, 'Armour', Macalister; Macalister; Goombungee; Cambooya; Mt Leinster, Dalby, in a well at 40 feet; 'Cardoch', near Dalby, at Por. 137, Par. St Ruth; Por. 137, Par. St Ruth; Freestone Creek; and from the eastern Darling Downs (particular localities unspecified).

SPECIFIC DIAGNOSIS: Species relatively large. Mandible moderately shallow, with symphysis elongate; symphysis ascends at low angle anteriorly; lateral groove on ramus extends posteriorly well below alveolar margin to below anterior root M_2 .

I_1 elongate, relatively markedly curved in occlusal view, with enamel produced into dorsolabial and ventrolingual flanges. P_2 relatively elongate, with longitudinal crest moderately high, mostly straight but curving slightly linguallly anteriorly; crest transected by two or three sets of vertical labial and lingual ridges; cuspules developed. DP_3 with relatively high lophids; broad, rounded ridge descends anteriorly from metaconid to anteriorly swollen base of protolophid; anterolabial fossette present; weak ridge descends anterolabially from entoconid to talonid base, close to midlink; posterior cingulum well defined. P_3 elongate, usually slightly constricted at posterior one-third, with longitudinal crest relatively high, straight or slightly convex linguallly; crest transected by three or four sets of vertical labial and lingual ridges; cuspules developed. Lower molars with high lophids; trigonid basin and anterior cingulum relatively narrow; anterolabial fossette

present; slight ridge descends from entoconid towards talonid; posterior cingulum normally present, well defined.

Upper incisors broadly U-shaped; I^1 moderately large, while I^3 elongate at distal edge. C^1 occasionally present, vestigial. P^2 relatively elongate, with crown margins converging anteriorly; longitudinal crest high, straight or slightly concave labially; crest transected by at least two sets of vertical labial and lingual ridges; cuspules present; lingual cingulum extends anteriorly to above paracone; cingulum slightly tumid in lingual view. DP^3 with high lophs, and occasionally with slight suggestion of forelink; strong, high ridge ascends anteriorly from paracone to labial limit of cingulum; posterior ridge from paracone ascends to unite across median valley with slight ridge from metaloph, partially closing off labial moiety of valley. P^3 elongate, being generally longer than M^4 , with crown markedly concave labially; longitudinal crest high, markedly to slightly concave labially; crest transected by two to four sets of vertical labial and lingual ridges; cuspules present; lingual cingulum continues anteriorly to above paracone; lingual ridge from first cuspule along crest usually prominent; cingulum markedly tuberculate in lingual view. Upper molars slightly constricted across median valley, with high lophs and usually no trace of forelink; strong ridge ascends anteriorly to limit of relatively narrow anterior cingulum; strong ridge usually curves posterolingually from paracone onto labial surface of midlink; occasionally slight anterior ridge present from metacone.

DESCRIPTION: Mandible moderately shallow, relatively thick; base of symphysis near planar, ascending at low angle anteriorly; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit relatively shallow, at posterior symphyseal limit; diastema elongate with diastemal crest posteriorly acute, more rounded anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen comparatively small, oval, close to diastemal crest about one-third distance along crest from P_3 to limit of ramus. Ramus with moderately deep lateral groove extending posteriorly to below anterior root of M_2 , usually disrupted by roots of P_3 ; groove positioned well below alveolar margin. Diagastric process separated from base of angle by very shallow post-diagastric sulcus, bounded above by shallow diagastric fossa; this fossa separated above from shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, with shelf angle not developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of alveolar margin; masseteric foramen moderately large, with deep masseteric fossa. Angle of mandible markedly inflected, flexed posteriorly at margin, broadly rounded posteriorly, ascending at high angle to posterior flared limit of masseteric crest. Anterior margin of coronoid process reclining at approximately 15° to vertical; condyle broadly rounded anteroposteriorly, near planar transversely, approximately oval in occlusal view.

I_1 elongate, deeply rooted; slightly curved in lateral view, markedly curved in occlusal view, developing subhorizontal facet of wear with upper incisors and mesial wear facet at tip by approximation with other lower incisor; root compressed, oval in section; crown subquadrantal in section, tapering and blade-like anteriorly, enamelled laterally,

this produced dorsolabially and ventrolingually into flanges; crown also enamelled ventromesially; distally, tip wears rapidly, ultimately producing broadly rounded anterior margin.

P₂ relatively elongate, approximately semi-circular to sublunate in occlusal view, with lingual surface occasionally weakly convex but usually nearly straight or slightly concave and labial surface markedly convex. Longitudinal crest secant, slightly to moderately strongly curving lingually in its posterior extension, and curving slightly lingually anteriorly; crest transected by two (50%, n = 20) or three (50%, n = 20) sets of vertical labial and lingual ridges with production of cuspules at crest; where third set developed, posterior ridges poorly defined; anterior cuspid of crest well defined, but posterior cuspid less well developed; base of crown somewhat tumid. Height of enamel frequently greater anteriorly than posteriorly.

DP₃ molariform, subtriangular in basal outline, unconstricted or slightly constricted across talonid basin, with lophids moderately high, slightly convex posteriorly. Hypolophid much broader than protolophid. Trigonid basin moderately narrow, its length being less than distance between lophids. Forelink moderately high, strong, curving anterolingually from protoconid to near mid-point of relatively low anterior cingulum, slightly labiad to axis of crown; broad, rounded ridge descends anteriorly from metaconid to anteriorly swollen base of protolophid in lingual moiety of trigonid, occasionally produced as ridge to lingual portion of anterior cingulum; labially, anterior cingulum unites with base of protolophid with production of anterolabial fossette; lingual moiety of trigonid pocket-like, near planar, but labial moiety descends at high angle into fossette. Midlink moderately high, strong, curving anterolingually from hypoconid across talonid basin to unite with short, posterior ridge from near midpoint of protolophid; weak ridge descending anterolabially from entoconid passes into talonid basin close to midlink, occasionally continuing across talonid to below metaconid; slight ridge usually descends posteriorly from metaconid into talonid; talonid basin sharply U-shaped, near planar, descending only slightly labially and lingually from midlink. Posterior cingulum well defined, ascending slightly lingually, with slight ridge ascending towards entoconid from extremity. Infrequently, cingulum extends only partially across posterior of hypolophid. Base of crown occasionally tumid, particularly at labial extremity of talonid.

P₃ elongate, robust, deeply rooted; crown subovate in basal outline but usually slightly constricted at posterior one-third; labial margin slightly convex, with lingual margin occasionally convex but usually near straight or rarely concave. Longitudinal crest secant, straight or slightly convex lingually, rarely slightly sinuous between anterior and posterior cuspids, slightly curving lingually in its posterior extension; crest transected by three (50%, n = 38) or four (50%, n = 38) major sets of vertical labial and lingual ridges with production of cuspules at crest; where fourth set developed, posterior ridges generally poorly defined; occasionally with small intermediary ridges developed at crest; anterior cuspid of crest well defined, but posterior cuspid less well developed; base of crown somewhat tumid. Height of enamel usually similar anteriorly and posteriorly.

M₁ < M₂ < M₃ < M₄; molars subrectangular in basal outline slightly constricted across talonid basin; lophids high, slightly convex posteriorly, with hypolophid broader than protolophid in M₁, approximately equal in M₂ and M₃, and generally considerably

narrower in M_4 . Trigonid basin relatively narrow, rarely broader, its length approximately equalling distance between lophids. Forelink moderately high, strong, curving anterolingually from protoconid to near midpoint of low, relatively narrow, anterior cingulum slightly labial to axis of crown; slight ridges descend anteriorly from metaconid towards trigonid, and posteriorly towards talonid basin; anterior surface of protolophid in lingual moiety of trigonid usually swollen; anterior cingulum usually descends at high angle from forelink, uniting with protolophid base, frequently defining anterolabial fossette; cingulum somewhat expanded anterolingually, but abruptly truncated; lingual moiety of trigonid near planar, but labial moiety descends at moderate to relatively high angle. Midlink moderately high, strong, curving anterolingually from hypoconid to unite with slight ridge from near mid-point of protolophid above talonid; slight ridge descends anterolabially from entoconid towards talonid; occasional slight ridges descend posterior surface of protolophid; talonid basin sharply U-shaped, near planar, descending only slightly labially and lingually from midlink. Posterior cingulum normally present, usually well defined, occasionally tumid, ascending lingually, frequently with slight ridge ascending towards entoconid from lingual extremity. Base of crown somewhat tumid, especially at labial extremity of talonid basin.

Cranium large, length being 289.8–290.3 ($n = 2$) in adult specimens; elongate, with rostrum only slightly tapered anteriorly, very slightly deflected, and somewhat inflated dorsolaterally; nasals extending well forward above premaxillae; maxillae dorsally in wide contact with frontals; laterally with infraorbital foramen simple, above posterior of P^3 in adult specimens, positioned well in advance of jugal; infraorbital canal elongate but variable, being 26.5–45.0 ($n = 8$); inferior process of anterior zygoma root moderately strong, extending ventrally almost to level of occlusion of cheek teeth. Lacrymal expanded onto facial surface, with superior and inferior lacrymal foramina on facial side of orbital rim; superior lacrymal tuberosity wide, bulbous, with inferior lacrymal tuberosity smaller, but prominent. Premaxillae with anterior narial floor declining posteriorly, wide; anterior premaxillary narial spines moderately strong. Labial foramen prominent, variably positioned, occasionally on ridge at edge of palate opposite posterior end of palatine foramen, but usually slightly mesiad to ridge, at premaxilla–maxilla suture. Palate entire, penetrated posteriorly by anterior palatine foramen and posterior lateral foramen; palatines moderately large, extending anteriorly to about level of M^3 in adult specimens. Jugal laterally excavated for superficial layer of masseter, with zygomatic arches converging somewhat anteriorly, with zygomatic crest posteriorly curving backwards and ventrally. Roof of braincase arched, with sagittal crest strongly defined in adult specimens owing to confluence of ridges passing posteriorly from above orbits. Subsquamosal foramen well defined, in strong squamosal sulcus separated below by continuation of zygomatic crest; squamosal widely separated from frontal, contributing with jugal, to glenoid fossa. Postzygomatic foramen prominent, at base of supratympanic sulcus in supratympanic fossa, immediately above external auditory meatus, separated from this by mastoid–squamosal crest. Mastoid foramen well defined towards upper limit of narrowly exposed mastoid. Post-glenoid process moderately strong, rather ovate posteriorly; post-glenoid foramen situated mesiad to process and at anterior limit of tympanic. External auditory meatus not well preserved, but moderately high; anteriorly bulla moderately crenulate;

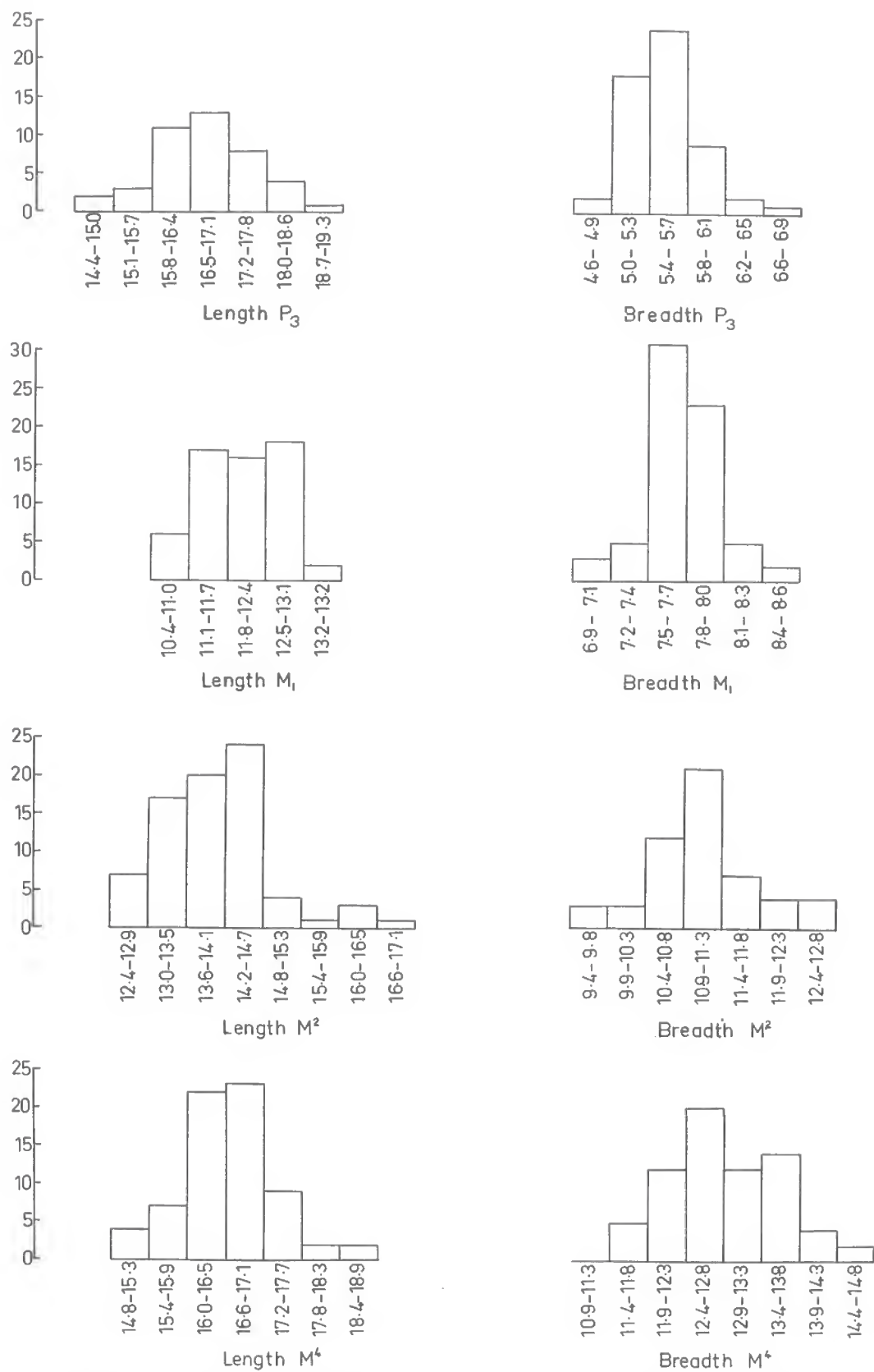


FIG. 5: Representative histograms for cheek teeth parameters in the *Protomnodon anak* Owen sample from the Pleistocene fluvial deposits of the eastern Darling Downs.

alisphenoid bulla slightly inflated. Tympanic extending only slightly down paraoccipital process; processes broken in all specimens, but strong. Well defined ovale crest developed anteriorly from mesial wall of foramen ovale, bordering pterygoid cavity; crest continues laterally around foramen ovale to alisphenoid bulla; pterygoid cavity with several small fenestrations. Basisphenoid broadly grooved posteriorly at mid-line, this extending on to anterior of basioccipital; entocarotid canal posterior to basisphenoid–basioccipital suture; pterygoids partially overlap basisphenoid, being in sutural contact. Petrosal with exposed surface mesial to eustachian canal gently concave posteriorly, sharply rounded anteriorly. Ridge extends mesially from paraoccipital process anterior to posterior lacerate foramen. Supraoccipital relatively low, wide, with lambdoidal crest extending posteriorly to marked extent with well defined supraoccipital depressions separated by moderate, rounded, median nuchal crest; inferior supraoccipital depressions absent. Condylod foramen prominent.

TABLE 1

MANDIBULAR MEASUREMENTS FOR *Protemnodon anak* OWEN

Specimen	P ₃	M ₁	M ₂	M ₃	M ₄
F3398*	16.2 × 6.0	— × 7.5	13.4 × 9.2	16.0 × —	16.6 × —
F3396**	16.8 × 5.4	10.5 × 7.5	13.5 × 9.4	16.3 × 10.5	17.8 × —

* Cast of holotype *P. anak*; ** Cast of holotype *P. og.*

Upper incisors broadly U-shaped in occlusal outline. I¹ large, with enamel surface from base to tip, longer than I² or I³, axially curved; directed anteroventrally and somewhat mesially with tips approximated; labial surface curved, with slight vertical groove present near anterior extremity of tip, and stronger groove present about one-third distance along occlusal surface from posterior limit; anteromesial surface moderately curved distally, becoming more broadly curved towards crown base; mesial surface unenamelled, broadly curved, while posterior surface gently concave. I² slightly more elongate along occlusal surface in unworn teeth than I¹; labial surface at tip marked by broad groove, about one-third distance along crown from posterior limit; this occasionally offset from sharper groove towards base of crown, near mid-line of labial surface; occlusal surface not known in unworn condition, but with well defined groove extending posteriorly and ascending posterolabial crown surface for short distance; posterolabial portion of crown flared slightly. I³ crown elongate distally, restricted basally, with broad, rounded, longitudinal groove towards base on labial surface and prominent diagonal groove across distal, posterolabial surface; this groove continues anteriorly along occlusal surface to terminate behind anterior surface; internally surface gently convex labially, but externally crown above occlusal groove flares posterolaterally.

TABLE 2
SUMMARY OF MEASUREMENTS FOR *Protenmodon anak* OWEN

Character	Maxillae				Mandibles					
	n	O.R.	\bar{X}	s	V	n	O.R.	\bar{X}	s	V
I ₁ Depth					21	12.8-16.3	14.8	0.8715	5.89
P ₂ length				—	20	10.2-11.8	11.0	0.4622	4.20
Maximum breadth				—	23	4.6- 5.7	5.3	0.2557	4.82
DP ₃ length	7	10.7-11.8	11.0	0.3719	3.38	32	9.0-11.8	10.6	0.5591	5.27
Breadth protoloph (-id)	6	8.0- 8.8	8.4	0.3193	3.80	25	5.3- 6.6	5.8	0.3187	5.49
P ₃ length	32	16.5-18.9	17.7	0.6674	3.77	42	14.7-18.8	16.7	0.9059	5.42
Maximum breadth	36	7.4-10.1	8.4	0.7258	8.64	55	4.7- 6.6	5.4	0.3874	7.17
M ₁ length	34	10.7-13.3	11.9	0.6896	5.79	59	10.4-13.5	12.0	0.7484	6.24
Breadth protoloph (-id)	36	9.1-11.2	10.0	0.4690	4.69	68	6.9- 8.6	7.7	0.3111	4.04
Height *	5	8.5-11.8	10.5	—	—	—	—	—	—	—
M ₂ length	54	12.9-15.3	14.1	0.6073	4.31	85	12.3-15.3	13.9	0.7469	5.37
Breadth protoloph (-id)	46	10.3-12.8	11.5	0.5262	4.58	79	8.1-10.1	9.3	0.3948	4.25
Height *	9	8.9-12.6	10.9	1.4217	13.04	31	7.0- 9.0	7.9	0.5313	6.73
M ₃ length	63	14.0-16.6	15.5	0.6257	4.04	98	13.8-16.8	15.5	0.6963	4.49
Breadth protoloph (-id)	51	11.0-13.7	12.3	0.6543	5.32	91	9.3-11.2	10.4	0.3911	3.76
Height *	16	7.7-12.4	10.9	1.1532	10.58	51	7.2- 9.1	8.3	0.5567	6.71
M ₄ length	35	14.4-17.5	16.0	0.1833	5.08	75	15.0-18.0	16.5	0.6987	4.23
Breadth protoloph (-id)	34	11.3-13.7	12.4	0.6555	5.29	73	9.7-11.9	10.8	0.4691	4.34
Height *	12	7.8-11.8	9.5	1.2232	12.88	47	6.2- 8.7	7.6	0.5316	6.99

*Enamel height measured at hypocone and entoconid in unworn teeth.

C¹ rarely present, extremely small, vestigial, laterally compressed.

P² relatively elongate, subovate to subtriangular in basal outline, being slightly to considerably broader posteriorly than anteriorly; longitudinal crest secant, moderately high, slightly concave labially or nearly straight; apex of paracone about one-quarter distance along crown from anterior point; crest transected by two sets of vertical labial and lingual ridges with production of cuspules at crest. Hypocone moderately high, being about one-half as high as metacone, united to metacone by strong, high labial ridge; posterior ridge from hypocone curves labially above base of crown to above metacone; shallow posterior fossette developed between this and ridge connecting posterior cusps. Anterior ridge from hypocone ascends sharply to form low lingual cingulum, converging anteriorly to above paracone, connected to it by slight ridge. Lingual cingulum gently convex lingually, occasionally sinuous, slightly tumid in lingual view; lingual basin shallow, subtriangular in shape, traversed by continuations of lingual ridges from cuspules at longitudinal crest. Slight anterolingual fossette formed in lingual basin. Weak ridge occasionally present at anterolingual base of crown.

DP³ molariform, subrectangular in basal outline, slightly constricted across median valley; lophs moderately high, slightly bowed anteriorly; metaloph broader than protoloph. Anterior cingulum low, relatively narrow and short, with slight suggestion of forelink above axis of crown, at base of descending protoloph; accessory ridges occasionally present across cingulum; cingulum somewhat tumescent lingually. Strong, high ridge ascends anterolingually from paracone to labial limit of anterior cingulum, this being most anterior point of crown. Midlink moderately strong and high, curving posterolabially from protocone to unite with short ridge from near mid-point of metaloph, above median valley; uniting with slight ridge from anterior surface of metaloph, partially closing off labial moiety of valley, about half-way between midlink and labial margin. Median valley sharply V-shaped labially and lingually. Strong ridge curves posterolabially from hypocone to base of crown above metacone, while weaker ridge curves posterolingually from metacone towards crown base, terminating labiad to axis; ridge from hypocone somewhat posteriorly flared, with slight posterior fossette formed at axis of crown.

P³ elongate, being longer than any molar, usually somewhat broader posteriorly than anteriorly; crown in occlusal view frequently markedly concave labially, but generally straight or slightly convex lingually; longitudinal crest secant, moderately high, markedly to slightly concave labially; apex of paracone about one-fifth distance along crown from anterior point; crest transected by three (51 %, n = 37), four (46 %, n = 37), or occasionally two (3 %, n = 37) sets of vertical labial and lingual ridges, with production of cuspules at crest. Hypocone moderately high, being about three-quarters as high as metacone, united to metacone by strong, high, labial ridge; posterior ridge from metacone ascends towards crown base; posterior ridge from hypocone curves labially to above metacone; well defined posterior fossette developed between this and ridge connecting posterior cusps. Anterior ridge from hypocone usually ascends sharply to form low, lingual cingulum, generally converging anteriorly to above paracone, connected to it by slight vertical ridge. Lingual ridge from first cuspule along crest from paracone generally prominent, separating anterior one-third of cingulum and lingual basin as slight anterolingual

pocket; occasionally other pockets developed posterior to this; in lingual aspect, cingulum markedly tuberculate, at points of origin of lingual ridges to crest cuspules. Lingual basin relatively shallow, separated by extensions of lingual ridges from crest. Base of crown somewhat tumid, particularly anteriorly.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, unconstricted or slightly constricted across median valley; lophs moderately high, slightly bowed anteriorly; metaloph slightly broader than proto-loph in M^1 , approximately equal or slightly narrower in M^2 and occasionally M^3 , and markedly narrower in remaining M^3 and M^4 . Anterior cingulum low, relatively narrow and short, sometimes broader, descending labially; generally no trace of forelink present; cingulum frequently somewhat tumescent lingually. Strong, high ridge ascends anteriorly from paracone to labial limit of anterior cingulum, with anterior margin of cingulum broadly rounded between labial and lingual limits; slight fossette usually present in anterolingual portion. Midlink moderately strong and high, curving posterolabially from protocone to unite with short ridge from near mid-point of metaloph, above median valley; strong ridge curves posterolingually from paracone usually on to labial surface of midlink, occasionally uniting with slight, variable ridge ascending anterolingually from metacone. Median valley narrowly U-shaped in labial moiety, more broadly U-shaped lingually; base of valley not markedly ascending labially or lingually from midlink. Strong, slightly flared ridge curves posterolabially from hypocone to base of crown slightly mesiad to posterolabial limit, uniting with weaker ridge ascending slightly posterolingually from metacone. Slight posterior fossette formed slightly labiad to axis.

TABLE 3
MEASUREMENTS FOR UPPER INCISORS IN *Protomnodon anak* OWEN

Specimen	F2540	F5176	F651	F2103	F5028	F3672	
						rt.	lt.
Length I^1	—	9.1	10.0	9.6	9.5	9.0	9.3
Length I^3	13.4	14.1	11.5	14.3	12.3	14.5	14.5

DISCUSSION: Owen (1859) introduced the name *Macropus anak* as a *nomen nudum* and later (Owen, 1873) used the combination *Protomnodon anak* in abstract in like fashion. The name *Protomnodon anak* was validated by Owen (1874) and dates from that time. Knowledge of the species is currently restricted to cranial remains.

In describing *P. anak*, Owen (1874) emphasized the comparatively broader trigonid basin (prebasal ridge) in M_4 in the holotype specimen and in the specimen figured (Owen, 1874, pl. 25, fig. 3). This feature is found to be somewhat variable where sufficient material is available to more fully assess the range in morphological variation present. As indicated by Owen (1874) the presence of a posterior cingulum (postbasal ridge) is variable, but it does prove to be present in most instances. Where absent in one molar, it is usually present in others of the same series.

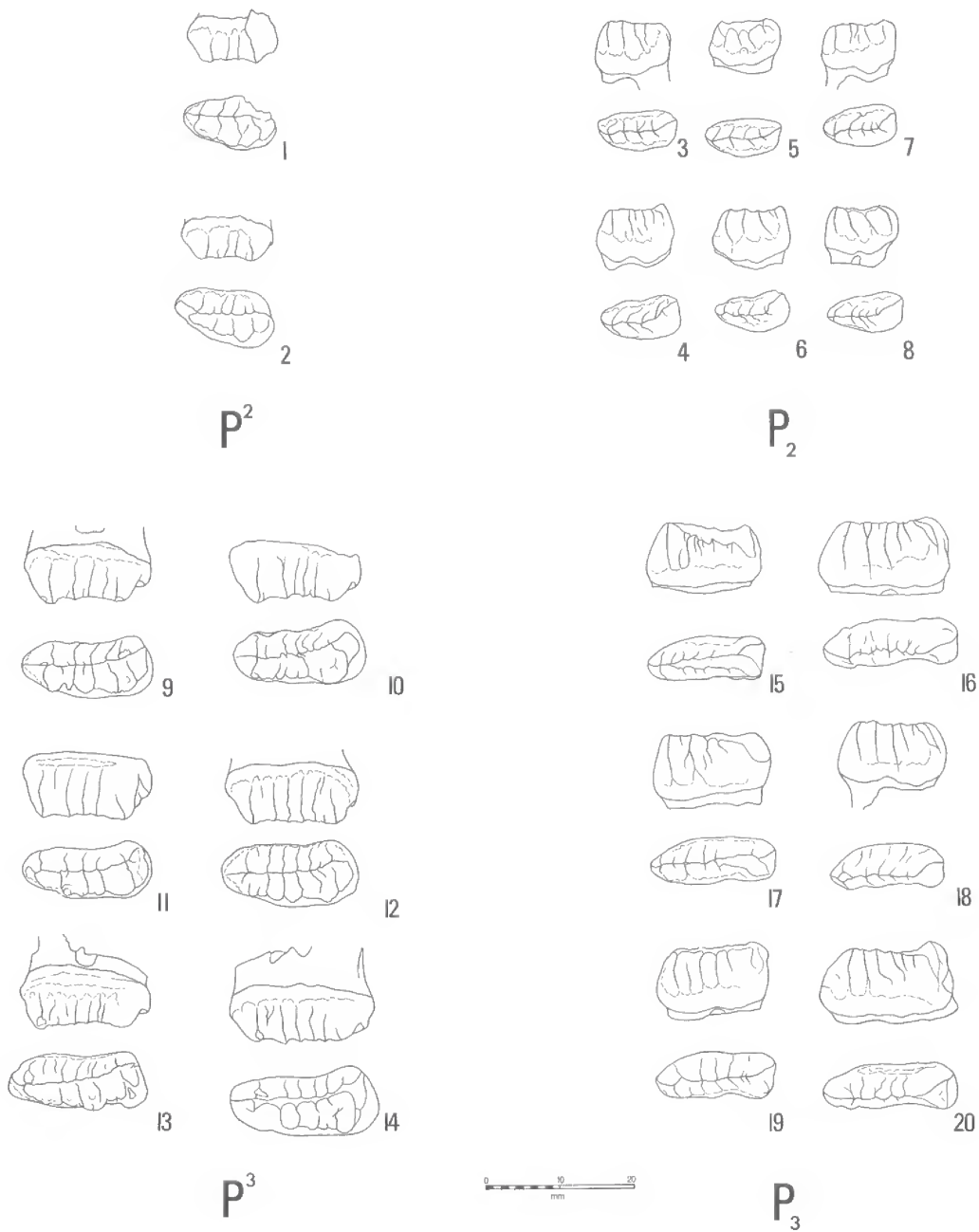


FIG. 6: Morphological variation in the premolar teeth in *Protamnodon anak* Owen. Lateral view above, occlusal view below. 1, right P^2 reversed, F5060; 2, left P^2 , F3677; 3, left P_2 , F4844; 4, left P_2 , F3046; 5, right P_2 reversed, F4818; 6, left P_2 , F3644; 7, left P_2 , F4832; 8, left P_2 , F4817; 9, right P^3 reversed, F5200; 10, left P^3 , F4977; 11, right P^3 reversed, F3667; 12, left P^3 , F5197; 13, left P^3 , F5045; 14, right P^3 reversed, F5178; 15, right P_3 reversed, F3003; 16, left P_3 , F2998; 17, right P_3 reversed, F3017; 18, left P_3 , F3006; 19, right P_3 reversed, F4900; 20, left P_3 , F4871.

Owen (1874) utilized several features to justify the separation of *P. og* Owen from *P. anak* here considered synonymous. These included the strength of the molar links and the inclination of the diastemal crest anterior to P_3 . Complete intergradation exists where the sample examined is sufficiently large. *P. og* was further distinguished from *P. anak* by its larger size. As indicated in the accompanying representative histograms, illustrated in Figure 5, no major size distinctions are present in the material. Measurements for the holotype specimens of *P. anak* and *P. og* are presented in Table 1. Table 2 presents the summaries of measurements for mandibular and maxillary specimens of *P. anak* and indicates only slight to moderate variation as expressed by the Coefficient of Variation (V) for all measurements except the height of enamel at the hypocone in unworn upper molar teeth. Generally, the values for V are consistent with those determined for the living Grey Kangaroo, *Macropus giganteus* Shaw and the Sandy Wallaby, *M. agilis* (Gould), by Bartholomai (1971) and for other fossil kangaroos from the Darling Downs area (Bartholomai, 1967, 1970). Slight age differences may be present between localities from which the sample was drawn but no control to evaluate the possible effect of this is possible at this time because of a lack of statistically significant samples from different sites.

The abnormal values for V in the heights of upper molar teeth are not mirrored in those for the corresponding lower teeth and the disparity appears to result not from an actual difference in height of crown, but from differences in the level of enamelization of the crown in the upper molars. Moderately high values for the Coefficient of Variation for the breadths of P_3 and P^3 reflect true variation in these characters in *P. anak*, also shown to be present in the living macropodids considered by Bartholomai (1971). This is true regardless of the fact that the permanent premolars in *P. anak* are large, functional teeth which have not been found excluded from the tooth row by progression. A forward movement of the tooth row is present, but it is not as marked as in the larger species of the genus *Macropus*. Morphological variation for the premolars in *P. anak* is illustrated in Figure 6.

Of interest is the fact that an upper canine is preserved in F3672, the only specimen in the Queensland Museum collections to present this tooth. It is small and vestigial, but morphologically it is similar to the C^1 developed in other macropodids. Its presence has not previously been recorded in *Protemnodon*.

The upper incisors, although not preserved in statistically useful numbers, present features which suggest their use in the separation of at least some of the species of *Protemnodon*, particularly in the separation of *P. anak* from specimens here referred to *P. roechus* Owen. Stirton (1963) indicates the marked discrepancy which occurs in *Protemnodon* in the lengths of the occlusal surfaces in I^1 when compared with the lengths in I^3 , but suggests that there appears to be intergradation between the extremes. While variation certainly exists, the present sample of *P. anak*, measurements for which are tabulated in Table 3, shows no overlap of values with those for *P. roechus* (Table 11). It is unfortunate, however, that upper incisors are at present unknown in the Queensland Museum collections in the medium to large sized species *P. brehus*, derived from the same sediments as *P. anak* and *P. roechus*.

A similar difference exists in the depth of the lower incisors, although the comparisons are valid only in relatively unworn specimens because of the extreme wear facets developed in these teeth. A summary of measurements for the depth of I₁ in *P. anak* is presented in Table 2. This shows marked differences from that for the corresponding tooth in *P. roechus*, results for which are presented in Table 10. However, some variation is evident within samples in these species and, in the absence of lower incisors in *P. brehus* the taxonomic value of these teeth is difficult to assess.

The crania of *P. anak* represented in the present sample agree well with the description provided in Stirton (1963). From his illustrations, it appears certain that the subject of his figure 2, AM F2221 is of *P. anak*. It has been shown above, however, that AM F16490, illustrated by Stirton (1963, fig. 3) is clearly not referable to this species. A reconstruction of the skull of *P. anak*, based on the present sample, is here presented in Figure 2.

Owen (1876, 1877) has described several fourth metatarsals and referred these to *P. anak* with no apparent justification. These are totally dissimilar in proportions to the metatarsals of *P. otibandus* Plane, illustrated by Stirton (1963), from the Pliocene Oti-banda Formation in New Guinea. Proportionately similar metatarsals to those found in *P. otibandus* are present in the Pleistocene fluvial deposits of the eastern Darling Downs but no attempt has been made at this time to sort these. It is certain, however, that the metatarsals in *P. anak* are represented in this disassociated material and that the specimens referred by Owen (1876, 1877) have been incorrectly assigned.

P. anak is the best represented species of *Protemnodon* in the Queensland Museum collections and has been recorded from numerous localities in the Pleistocene fluvial deposits of the eastern Darling Downs. It is, as yet, unknown from other Queensland localities, although a mandibular specimen, F2496, from Chinchilla, appears to be referable to the species. Preservation of this specimen is unlike that normally associated with material derived from the Chinchilla Sand (Woods, 1956), and it is probable that it was collected from Pleistocene terrace deposits in the area.

Tedford (1967) indicates the presence of a species of *Protemnodon* smaller than *P. brehus* Owen from the Scotchtown Cave assemblage in northwestern Tasmania (Gill and Banks, 1956), but as no illustration or description has yet been presented for this material its specific identity must remain in doubt. A mandibular ramus from King Island, in Bass Strait, morphologically similar to the Scotchtown Cave material (Tedford, 1967), has been referred to *Macropus anak* by Scott and Lord (1924), who state that it is closely comparable with the specimen figured by Owen (1874, pl. 25, figs. 7–10) as *P. anak*. As such, it is very likely that it is referable to this species. However, the ramus was not figured and again the specific determination cannot be resolved at this time.

It is apparent from the material figured and described by Stirton (1963) that *P. anak* is present in the Wellington Caves fauna and several specimens of this species were located in the small sample of *Protemnodon* currently available in the Australian Museum collections and which unquestionably came from that deposit. *P. anak* is widespread in New South Wales and is present from Weetalabah Creek, near Coolah; Breeza; Copes Creek; Huntsgrave, Keepit, in a deposit thirty feet below the surface; in a well at Parsens

Hill Plain, Warrah; Abercrombie Caves; and from nine miles west of Attunga. Morphological variation exhibited within this material is similar to that seen in the Queensland sample, but too few specimens are available to allow statistical comparison of samples to be undertaken.

In Western Australia, *Macropus anak* is recorded by Glauert (1912) from the Mammoth Caves in the southwest, but he does not illustrate either of the two mandibular fragments mentioned. From his discussion, it appears that the material may not be of *P. anak* and that it may be comparable with *P. brehus*. The specimens later recorded by Glauert (1921) as *Macropus anak*, from Quambun Station, Fitzroy River Crossing in northwestern Western Australia, are also doubtfully referable to the species until checked.

Stirton *et al.* (1961) recorded the presence of a small species of *Protemnodon*, comparable with *P. og*, from the Pleistocene Malkuni Fauna of the Katipiri Formation from the Tirari Desert, in northeastern South Australia, but suggested the material from the older Kanunka Fauna from that Formation may be distinct.

It is thus apparent that although the species may be widely represented throughout Australia, the distribution is largely obscured by uncertainty in identification of referred specimens.

***Protemnodon brehus* (Owen, 1874)**

(Plates 13–15)

Sthenurus brehus Owen, 1873, p. 128 (*nomen nudum*).

Protemnodon mimas Owen, 1873, p. 128 (*nomen nudum*).

Sthenurus brehus Owen, 1874, pp. 272–4, pl. 27, figs. 5–9; 1876 (*partim*), pp. 212–8, pl. 28, figs. 1–3; 1877, pp. 424–6, 442, 444, pl. 87, figs. 5–9; Etheridge Jnr., 1892, p. 678; Simpson, 1930, p. 77.

Protemnodon mimas Owen, 1874, pp. 278–80, pl. 26, figs. 1–3; 1877, pp. 431–3, 447–9, pl. 86, figs. 1–3; Etheridge Jnr., 1892, p. 677; Palmer, 1904, p. 883; Simpson, 1930, p. 76; Stirton, 1963, p. 139, fig. 14a.

Macropus brehus (Owen): Lydekker, 1887, pp. 207, 309, 311; Lydekker, 1894, pp. 256–7; Lydekker, 1896, p. 256.

Halmaturus anak (Owen): De Vis, 1895 (*partim*), pp. 104–9.

Protemnodon brehus (Owen): Stirton, 1963, p. 141, fig. 15b; Tedford, 1967, pp. 97–109, figs. 25–6.

MATERIAL: F3400, cast of holotype of *P. brehus* (Owen), British Museum (Natural History) No. 43303a, partial palate with left M¹–M⁴, right M³–M⁴, adult, Wellington Valley, N.S.W., figd Owen (1874, pl. 27, figs. 5–6; 1877, pl. 87, figs. 5–6).

F3395, casts of holotype of *P. mimas* Owen, British Museum (Natural History) No. 43351, partial left mandibular ramus, with P₃–M₄, adult, Gowrie Creek, SE. Q., figd Owen (1874, pl. 26, figs. 1–3; 1877, pl. 86, figs. 1–3).

Five juvenile mandibular rami, 19 adult mandibular rami, 2 isolated lower teeth, 2 juvenile maxillae, 13 adult maxillae, and 4 isolated upper teeth from the following localities in the eastern Darling Downs: King Creek; King Creek, at M.R. 873335 Clifton 1 mile map; King Creek, at M.R. 055459 Clifton 1 mile map; Ravensthorpe, Pilton; 'Sharrow' (Harrow, Cambooya); Gowrie; Jimbour Creek, near Dalby; Kaimkillenbun, near Dalby, 54 feet below surface; and from the eastern Darling Downs (particular localities unspecified).

Other Queensland localities represented include 'Coreena', between Barcaldine and Aramac, C.Q.; and 'Planet Downs', near Gregory Downs, NE. of Camooweal, N.W.Q., 17 feet below surface.

SPECIFIC DIAGNOSIS: Large species, generally larger than *P. anak*.

Mandible relatively deep, with symphysis elongate; symphysis elevated to approximately 20° to base of mandible; lateral groove extends posteriorly to below M_2-M_3 , moderately close to alveolar margin.

P_2 relatively elongate, with longitudinal crest high, nearly straight except in posterior one-quarter where crest markedly flexed lingually; crest transected by one set of near vertical labial and lingual ridges. DP_3 unconstricted across talonid basin; trigonid basin very broad; posterior cingulum strongly developed, broad. P_3 relatively elongate, broader posteriorly, with longitudinal crest high; crown usually strongly constricted lingually at posterior one-third; crest straight but rapidly curving lingually in posterior extension, transected by three to four sets of vertical labial and lingual ridges; cuspules present. Lower molars slightly constricted across talonid basin, with lophids high; trigonid basin and anterior cingulum broad; anterolabial fossette present; posterior ridge from metaconid not developed; slight ridge occasionally present from entoconid; posterior cingulum well defined, broad.

P^3 relatively elongate, being generally shorter than length of M^4 ; crown slightly concave labially in occlusal view; longitudinal crest high, slightly concave labially; crest transected by three or four sets of vertical labial and lingual ridges; cuspules present; lingual cingulum occasionally continues anteriorly from above paracone to near anterior of crown; cingulum markedly sinuous in lingual view. Upper molars slightly constricted across median valley, with high lophs; anterior cingulum broad, anteriorly broadly curved; forelink generally absent; anterior ridge from paracone strong, usually passing to limit of cingulum; relatively strong ridge curves posteriorly from paracone, often continuous across valley with lesser ridge from metacone; base of median valley near planar transversely; lingual limit of valley usually not tuberculate.

DESCRIPTION: Mandible relatively deep and thick; base of symphysis elevated at approximately 20° to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit relatively deep, near posterior symphysial limit; diastema relatively elongate with crest acute, becoming slightly less so anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen relatively large, ovate, close to diastemal crest. Ramus with well defined, shallow, lateral groove extending posteriorly to below M_2-M_3 , often disrupted by roots of P_3 ; groove positioned about one-quarter distance from alveolar margin to base of ramus. Diagastric process bounded above by shallow diagastric fossa; this fossa separated above from shallow depression opening posteriorly into large pterygoid fossa. Post-alveolar shelf short, with shelf angle usually not well developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above mandibular foramen. Masseteric crest raised to about level of alveolar margin; masseteric foramen moderately large, with masseteric fossa relatively deep. Coronoid process, condyle and angle of mandible not preserved in any specimen.

I_1 not preserved.

P_2 relatively elongate, slightly broader posteriorly than anteriorly. Longitudinal crest secant, nearly straight, except in posterior one-quarter, where crest is markedly

flexed linguallly; crest transected by one major set of near-vertical labial and lingual ridges; anterior cuspid of crest well defined. Base of crown slightly tumid, especially linguallly.

DP₃ molariform, subrectangular in occlusal view, unconstricted across talonid basin, with protolophid narrower than hypolophid. Trigonid basin very broad, elongate. Forelink well defined, extending anteriorly to near midpoint of relatively low anterior cingulum; slight fossette present at margin of labial moiety of trigonid basin. Midlink moderately strong, extending anteriorly from hypolophid to near midpoint of protolophid, across talonid basin; basin shallowly U-shaped both labially and linguallly. Moderate ridge descends posteriorly from entoconid to lingual margin of strong posterior cingulum; posterior cingulum broad, extending and descending slightly from posterolingual crown margin to posterolabial margin.

P₃ relatively elongate, high, robust, deeply rooted; crown suboval to subtriangular in occlusal view, usually broader posteriorly than anteriorly and tapering anteriorly, but with slight to marked lingual constriction at about posterior one-third. Crest secant, nearly straight or slightly sinuous, markedly curving linguallly in its posterior extension; crest transected by three or occasionally four sets of vertical labial and lingual ridges with production of cuspules at crest; strength of ridges and cuspules decreases posteriorly. Anterior ridge from anterior cuspid of crest descends at moderately high angle to crown base. Base of crown slightly tumid. Height of enamel usually similar anteriorly and posteriorly.

M₁ < M₂ < M₃ < M₄; molars subrectangular in basal outline, usually slightly constricted across talonid basin; lophids high, slightly convex posteriorly, with hypolophid broader than protolophid in M₁ and M₂, approximately equal in M₃ and narrower in M₄. Trigonid basin broad, elongate, its length approximating distance between lophids. Forelink relatively high, moderately strong, curving anterolingually from protoconid to near midpoint of low, broad, anterior cingulum; cingulum gently curved to below protoconid, but more abruptly curved linguallly; trigonid basin normally descends at about same angle labially and linguallly from forelink, with slight anterolabial fossette formed at margin of labial moiety; very slight ridge descends anteriorly from metaconid but posterior ridge is not developed; this is sometimes accompanied by a posterolabial groove; midlink moderately high and strong, curving anterolingually from hypoconid to unite with short ridge from near midpoint or slightly labiad to axis of protolophid, above talonid basin; slight ridge occasionally present but sometimes quite strongly developed, descending anterolabially from entoconid, into talonid close to midlink; talonid basin sharply U-shaped, occasionally becoming more angular, descending at moderate angle labially and linguallly from midlink. Slight posterior ridge from entoconid usually

TABLE 4
MANDIBULAR MEASUREMENTS FOR *Protomnodon brehus* (OWEN)

Specimen	P ₃	M ₁	M ₂	M ₃	M ₄
F3395*	16.5 × 6.4	13.4 × —	15.3 × 10.6	17.9 × 12.1	19.7 × 12.3

* Cast of Holotype *P. mimas*.

present descending to unite with lingual limit of posterior cingulum, frequently mirrored by similar ridge from hypoconid; posterior cingulum well developed, nearly horizontal, broad, extending over most of posterior of base of hypolophid. Base of crown rarely tumid.

Cranium known only from maxillary fragments. Inferior process of anterior zygoma root moderately strong, extending to about level of occlusion of cheek teeth; infraorbital canal moderately elongate; palate entire, perforated by anterior palatine foramen and posterior lateral foramen.

DP³ imperfectly preserved. Only upper permanent cheek teeth sufficiently well known to be described.

P³ elongate, being generally slightly shorter than length of longest molar, slightly to moderately broader posteriorly than anteriorly; crown in occlusal view, slightly concave labially, slightly convex to nearly straight or even concave lingually; longitudinal crest secant, slightly concave labially, moderately high. Apex of paracone about one-fifth distance along crown from anterior point; crest transected by three or occasionally four sets of vertical labial and lingual ridges, with production of cuspules at crest; cuspules decrease in strength posteriorly, as do transecting ridges. Hypocone moderately strong, united to above metacone by strong, high, labial ridge; posterior ridge from metacone ascends towards crown base; posterior ridge from hypocone curves labially to above metacone; well defined posterior fossette developed between this and ridge connecting posterior cusps; anterior ridge from hypocone curves lingually and ascends sharply to form low lingual cingulum, generally only slightly converging anteriorly to above paracone, but occasionally further extending anterior to this point to unite with marked anterolingual ridge descending from anterior ridge from paracone; cingulum occasionally disrupted anteriorly; paracone connected to cingulum by moderately strong lingual ridge; in lingual view, cingulum markedly sinuous in outline. Ridges from cuspules along crest usually cross relatively shallow lingual basin, to cingulum; anterolingual fossette, posterior to ridge from paracone to cingulum, frequently well developed. Base of crown slightly tumid; enamel height usually slightly greater anteriorly than posteriorly.

M¹ < M² < M³ < M⁴; molars subrectangular in basal outline, slightly constricted across median valley; lophs moderately high, slightly bowed anteriorly; metaloph broader than protoloph in M¹, approximately equal in M² and M³, and narrower in M⁴. Anterior cingulum low, broad, short, near planar transversely; generally no trace of distinct forelink present, but ridgelets frequently pass from base of protoloph onto cingulum; anteriorly, cingulum flattened or very broadly curved; relatively strong ridge ascends from paracone, usually uniting with labial limit of cingulum, delimiting extent of cingular shelf; anterolingual fossette generally present at lingual limit of cingular shelf. Midlink moderately strong, relatively high, curving posterolabially from protocone to unite with short ridge from near mid-point of metaloph, above median valley; relatively strong ridge curves posterolingually from paracone to near midlink, often continuous across median valley with slight anterolingual ridge from metacone; labial moiety of median valley narrowly U-shaped, lingual moiety broadly U-shaped; base of valley near planar transversely; lingual limit of valley generally smooth, but very occasionally tuberculate. Strong, slightly flared ridge curves posterolabially from hypocone to base of crown slightly

mesiad to posterolabial limit, uniting with weaker ridge ascending slightly posterolingually from metacone. Slight posterior fossette formed between ridges and base of meta-loph, labiad to crown axis.

TABLE 5
MAXILLARY MEASUREMENTS FOR *Protemnodon brehus* (OWEN)

Specimen	M ²	M ³	M ⁴
F3400 lt.*	15.6 × 14.6	19.1 × —	17.6 × 14.1
rt.*	—	— × 14.2	17.4 × 13.9

* Cast of Holotype *P. brehus*.

DISCUSSION: *Sthenurus brehus*, described by Owen (1874), is the only species now referable to the genus *Protemnodon* based on maxillary remains, and represents the only Pleistocene species based on material collected from an area outside the Pleistocene fluviatile deposits of the eastern Darling Downs. Because of problems of association of maxillary and mandibular specimens of the genera *Sthenurus* and *Protemnodon*, the description of *S. brehus* contributed to the early confusion detailed by Stirton (1963). Both Lydekker (1887) and De Vis (1895) recognized the correct relationships of the species but referred it to the genera *Macropus* and *Halmaturus*, respectively. The former generic concept is here considered too broad, while the latter is nomenclaturally unavailable, constituting as it does a junior secondary homonym of *Macropus*. No doubt exists regarding the relegation of the species to the genus *Protemnodon*. The limits placed on the species by Lydekker (1887) are considered correct, whereas those of De Vis (1895), who referred all the Queensland material to a single species, *Halmaturus anak*, are too wide.

Queensland Museum specimens collected from the Darling Downs deposits have been checked against topotypic specimens in the Australian Museum, Sydney, from the Wellington Caves area and against a cast of the holotype, British Museum (Natural History) No. 43303a, and have been found to be morphologically inseparable. Minor size differences, although not able to be assessed statistically, appear to be within the limits expected for a single species.

Owen's (1874) description of *P. brehus* was based on two specimens, the holotype and a paratype maxillary fragment from the Wellington Caves, now numbered British Museum (Natural History) No. 43653. Tedford (1967) provides a redescription of this latter specimen (figured Owen, 1874, pl. 27, figs. 7–9). This differs to some extent from the material here referred, particularly in the lack of well defined subdivision of the lingual basin by ridges between the base of the longitudinal crest and the lingual cingulum. This character proved variable in the sample considered by Tedford (1967) from Lake Menindee, New South Wales, and it is apparent that the same is true of the Queensland sample. It is more usual, however, for the basin to be subdivided.

Among material subsequently described and figured by Owen is a partial skull which provides additional information on the morphology of *P. brehus*. This specimen,

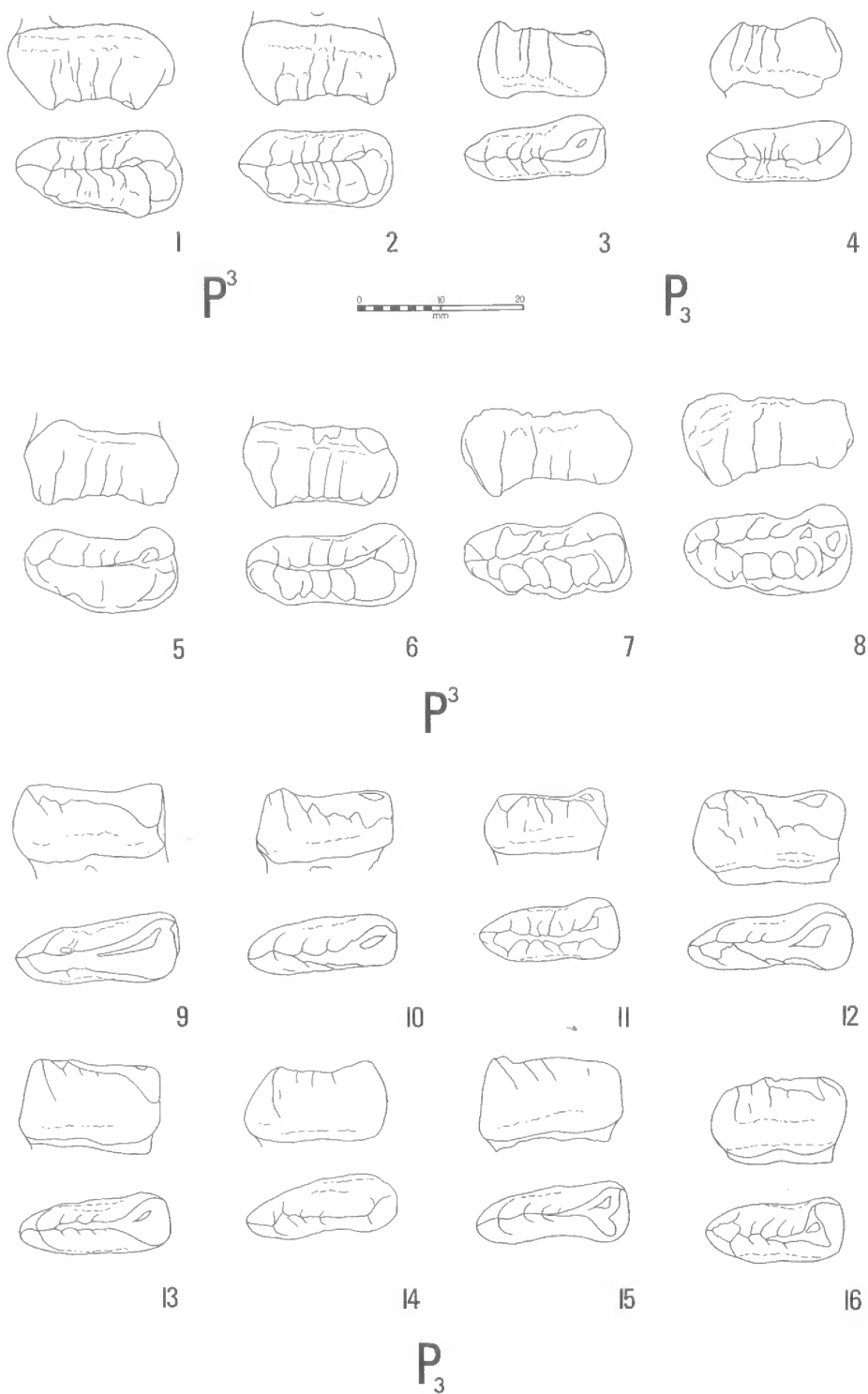


FIG. 7: Morphological variation in the permanent premolar teeth in *Protetmodon brehus* (Owen), (1–4) and *Protetmodon roechus* Owen (5–16). Lateral view above, occlusal view below. 1, left P^3 , F4795; 2, left P^3 , F4954. 3, left P_3 , F4941; 4, right P_3 reversed, F3651; 5, right P^3 reversed, F1384; 6, left P^3 , F1849; 7, left P^3 , F4971; 8, right P^3 reversed, F4955; 9, right P_3 reversed, F5077; 10, left P_3 , F5; 11, right P_3 reversed, F3009; 12, right P_3 reversed, F5078; 13, right P_3 reversed, F3033; 14, left P_3 , F3007; 15, right P_3 reversed, F3019; 16, right P_3 reversed, F5087.

TABLE 6
SUMMARY OF MEASUREMENTS FOR *Protomnodon brehus* (OWEN)

Character	Maxillae					Mandibles				
	n	O.R.	\bar{X}	s	V	n	O.R.	\bar{X}	s	V
P ₂ length	—	—	—	—	—	1	11.5	11.5	—	—
Maximum breadth	—	—	—	—	—	1	5.9	5.9	—	—
DP ₃ ^l length	1	12.3	12.3	—	—	1	11.6	11.6	—	—
Breadth protoloph (-id)	—	—	—	—	—	1	7.8	7.8	—	—
P ₃ ^l length	9	18.1–19.8	19.2	0.5339	2.78	10	16.4–18.7	17.7	0.8478	4.79
Maximum breadth	10	9.3–10.6	10.0	0.5011	5.01	9	6.5–8.2	7.1	0.4847	6.83
M ₁ ^l length	6	12.7–14.6	13.6	0.6899	5.07	9	12.0–14.8	13.5	0.9151	6.78
Breadth protoloph (-id)	4	12.0–12.7	12.3	0.2943	2.39	6	9.3–10.6	9.9	0.5099	5.16
M ₂ ^l length	14	14.8–17.0	16.3	0.6251	3.83	14	14.9–18.0	16.3	0.9231	5.66
Breadth protoloph (-id)	11	13.4–14.6	14.0	0.3420	2.44	11	10.6–12.7	11.5	0.6299	5.48
Height *	4	10.6–13.9	12.2	1.3699	11.23	3	9.6–9.9	—	—	—
M ₃ ^l length	18	16.2–18.1	17.5	0.5850	3.34	15	16.7–19.9	18.2	0.8311	4.57
Breadth protoloph (-id)	15	13.7–15.1	14.5	0.4017	2.77	13	11.9–13.2	12.6	0.4031	3.20
Height *	6	9.7–13.0	11.6	1.1849	10.21	6	8.2–10.6	9.7	0.8000	8.25
M ₄ ^l length	12	17.3–19.1	18.2	0.5885	3.23	11	18.1–20.6	19.2	0.8614	4.49
Breadth protoloph (-id)	11	13.7–15.0	14.3	0.4147	2.90	9	11.6–13.5	12.7	0.6041	4.76
Height *	4	9.8–12.2	11.1	1.1369	10.24	4	8.7–10.0	9.4	0.6055	6.44

* Enamel height measured at hypocone and entoconid in unworn teeth.

numbered 47833 in the British Museum (Natural History) collections possesses a full but worn complement of upper incisors and a right P^3-M^1 . Sufficient of the cheek teeth is preserved to indicate the correct reference of this specimen, collected from Clifton, Darling Downs, to *P. brehus*. The upper incisors appear to be somewhat intermediate in morphological detail between *P. anak* and *P. roechus* described below. I^1 is considerably larger than in *P. anak* compared with I^2 and I^3 . In lateral view the occlusal surfaces are angled considerably from the horizontal, more so than in *P. roechus*, while the diastemal length is somewhat shorter than in that species. The nasals appear to have been considerably retracted, similar to the situation in *P. roechus* and this conclusion is supported by a cranial specimen of *P. brehus* from Lake Tandau in the Lower Darling region of New South Wales, housed in the collections of the Western Australian Museum.

Lydekker (1887) has indicated that the cranial specimen illustrated by Owen (1874, p. 27, figs. 1–4) as *P. mimas* is of *P. brehus* but the specimen is not sufficiently well illustrated to allow this conclusion to be supported confidently. It is doubtful whether the premaxillae figured by Owen (1876, pl. 28, figs. 1–3) as *P. brehus* relate to this species. Morphologically, these appear referable to *P. roechus*.

Association of mandibular remains with the referred maxillary specimens has been achieved largely through considerations of size as well as morphology. Mandibular rami in the Queensland Museum collections here referred to *P. brehus* are morphologically identical with the holotype of *P. mimas*, described by Owen (1874) from Gowrie Creek, Darling Downs and, as suggested by Lydekker (1887), this species is here regarded in synonymy with *P. brehus*. Measurements for holotype specimens of *P. brehus* and *P. mimas* are presented in Tables 4 and 5.

Summaries of measurements for the Queensland sample of *P. brehus*, presented in Table 6, generally indicate only slight to moderate variation as expressed by the Coefficient of Variation, and are largely consistent with the values for V present in other fossil macropodids from the area, and in the control samples of recent macropodids the results of which were published in Bartholomai (1971). As with other species of *Protemnodon* here considered, the breadth of P^3 is moderately variable, whereas the heights of enamel at the hypocone in unworn teeth often suggest a high degree of variation. As suggested previously, however, high values of V for enamel height are influenced not by actual crown heights but by wide flexibility in the level of enamelization of the crown. Measurements for lengths and breadths of teeth generally fall within the values for V indicated by Simpson *et al.* (1960), as consistent for a single fossil species from slightly differing stratigraphic levels. Figure 7 illustrates some morphological variation present in permanent premolars.

Measurements for specimens referred to *P. brehus* by Tedford (1967) from Lake Menindee, often indicate sizes exceeding these for specimens in the Queensland sample. Because of the relatively small size of Tedford's (1967) samples, the statistical significance of these size differences cannot be evaluated. It is possible that there could be some representation in the Lake Menindee sample of the large species, *P. roechus*, considered below, and this could account for some of the larger values present in teeth dimensions.

Further morphological evidence more characteristic of *P. roechus*, particularly the tuberculation at the lingual extremity of the median valley in upper molars, is also apparently present to some extent in the sample.

Comparison of the Queensland material with a limited selection of specimens from the Bingara deposits, northern New South Wales, held in the collections of the Australian Museum, Sydney, indicates the presence of possible minor differences related to the breadth of anterior lower permanent cheek teeth. Morphologically, the Bingara and Darling Downs samples are identical and the size differences, relating as they do to a limited number of specimens in the available Bingara sample, are not considered sufficient to justify a suggestion of taxonomic distinction. Unfortunately, the maxillary sample available contains posterior cheek teeth only and the presence of minor size differences in the anterior cheek teeth cannot be confirmed in the upper dentition. Measurements for the Bingara material are included in Tables 7 and 8.

TABLE 7
MANDIBULAR MEASUREMENTS FOR *Protemnodon brehus* (OWEN)—BINGARA, N.S.W. SAMPLE

Specimen	P ₃	M ₁	M ₂	M ₃	M ₄
AM MF1092	—	—	—	18.0 × 12.2	—
AM F55351	—	—	—	—	19.4 × 13.3
AM F55352	—	—	—	18.6 × 12.4	—
AM MF1094	—	—	16.3 × 10.9	—	—
AM F55353	17.7 × 7.1	13.4 × 9.8	—	—	—
AM F55354	—	—	16.8 × 11.4	—	—
AM F55355	16.8 × 6.2	13.7 × 9.2	—	—	—
AM MF1057	—	—	15.7 × 11.7	—	—
AM MF1093	—	—	16.6 × 10.8	—	—

TABLE 8
MAXILLARY MEASUREMENTS FOR *Protemnodon brehus* (OWEN)—BINGARA, N.S.W. SAMPLE

Specimen	M ²	M ³	M ⁴
AM F55356	—	16.7 × —	18.7 × 14.4
AM F55357	—	—	18.7 × 15.2
AM F55358	16.4 × 13.3	—	—
AM F55359	15.4 × 13.6	—	—
AM F55360	16.6 × 13.9	—	—
AM F55361	16.3 × 13.9	—	—

In addition to cranial specimens, Owen (1877) also referred a disassociated distal end of a left femur to *P. brehus*. Further post-cranial material, including the pelvis, fibula, astragalus, cuboid, navicular, cuneiforms and metatarsals are described for the species by Tedford (1967). There is no evidence to support the reference of the femur by Owen (1877) and as indicated previously, there is some possibility that there may be more than one species of *Protemnodon* represented in the cranial remains from the Lake Menindee deposits. Undoubtedly, the pes material referred by Tedford (1967) is of *Protemnodon* by comparison with the remains figured by Plane (1967) for *P. otibandus* from the Pliocene Awe Fauna, New Guinea, but the specific identification of the referred specimens while probably correct would best await verification of the presence of only one species of *Protemnodon* in the Lake Menindee area.

Two mandibular specimens, F3028 and F4942 in the Queensland Museum collections, although generally agreeing morphologically with the species, have not been able to be assigned conclusively to *P. brehus*. These specimens exhibit marked reduction in the breadth of the anterior cingulum, a feature not showing intergradation with the referred sample at this time.

P. brehus is separable from *P. anak* by a consideration of both size and morphology. Separation by size alone is not conclusive, as a degree of overlap for particular characters is encountered. Where more than one tooth is preserved in a specimen, additional checks can be made for overlap with *P. anak* and by this means the bulk of the sample may be defined. No single morphological feature is sufficient to diagnose *P. brehus* and as many characters as possible must be considered before assignment is made. Among the more important morphological features of use in the separation of *P. brehus* from *P. anak* are the much broader nature of P^3 , the less concave nature of its labial surface, the broader extent of its lingual basin and the extension in the length of the lingual cingulum. The upper molars are morphologically similar but the anterior cingular shelf is more planar transversely. The mandibular symphysis is greatly elevated with respect to the base of the mandible while the labial groove is usually relatively closer to the alveolar margin. P_2 in *P. anak* is only slightly flexed lingually in the posterior extension of its longitudinal crest, while that in *P. brehus* is markedly flexed and approaches 90° in some specimens. In *P. brehus*, the trigonid basin in DP_3 is more planar transversely. As with the deciduous lower premolar, the longitudinal crest in P_3 is usually flexed to a greater extent than in *P. anak*, while the crown is broader posteriorly and more usually subtriangular than suboval in occlusal view. Lower molars are morphologically similar but the posterior cingulum tends to be more consistently better developed in *P. brehus*.

P. brehus is moderately widely distributed throughout Australia and apart from the records of the species in New South Wales already noted, the species is present from Cunningham Creek, County of Harden and from Lake Tandau in the lower Darling Region. Tedford (1967) indicates the presence of material compared with *P. brehus* at Curramulka, on Yorke Peninsula, and from the Warburton River, near Cowarie Station, in South Australia. Material from the Mammoth Cave in Western Australia also appears comparable with *P. brehus* (Tedford, 1967). The species is not yet recorded from Victoria and Tasmania.

Protemnodon roechus Owen, 1874

(Plates 16–19)

Protemnodon roechus Owen, 1873, p.128 (*nomen nudum*).*Protemnodon roechus* Owen, 1874, p. 281, pl. 27, figs. 10–13; 1877, p. 434, pl. 87, figs. 10–13; Palmer, 1904, p. 883.*Protemnodon antaeus* Owen, 1877, pp. 448–9, pl. 110, figs. 1–5; Etheridge Jnr., 1892, p. 766; Simpson, 1930, p. 76; Stirton, 1963, pp. 141–2, fig. 14b.*Macropus raechus* (Owen): Lydekker, 1887, pp. 212–3; 1894, p. 257; 1896, p. 257.*Protemnodon raechus* Owen: Etheridge Jnr., 1892, p. 678; Simpson, 1930, p. 76; Stirton, 1963, p. 142, fig. 15a.

MATERIAL: F3868, cast of holotype of *P. roechus* Owen, British Museum (Natural History) No. 35968, partial left mandibular ramus with P_3 – M_3 , adult, Gowrie, Darling Downs, (figd Owen, 1874, pl. 27, figs. 10–13; 1877, pl. 87, figs. 10–13).

F3397, cast of holotype of *P. antaeus* Owen, British Museum (Natural History) No. M2258, partial left mandibular ramus with P_3 – M_4 , adult, Queensland, (figd Owen, 1877, pl. 110, figs. 1–5).

Eleven juvenile mandibular rami, 39 adult mandibular rami, 6 isolated lower teeth, one nearly complete cranium, 2 premaxillae, 2 juvenile maxillae, one palate, 18 adult maxillae and 4 isolated upper teeth from the following localities in the eastern Darling Downs: King Creek; King Creek, Pilton; King Creek, Ravensthorpe, Upper Pilton; King Creek, Ravensthorpe, Pilton, at M.R. 190398 Liverpool Range 1 mile map; King Creek, at M.R. 045455 Clifton 1 mile map; King Creek, near M.R. 039454 Clifton 1 mile map; King Creek, at M.R. 134443 Liverpool Range 1 mile map; Clifton; King Creek, at M.R. 128445 Liverpool Range 1 mile map; Wellcamp, Darling Downs; Freestone Creek, Warwick; Gowrie Creek; Gowrie; Macalister; near Dalby; Condamine River, at M.R. 403644 Dalby 4 mile map; and from the eastern Darling Downs (particular localities unspecified).

Other Queensland localities represented include Russenden Caves, near Glen Lyon Caves, Pikes Creek, Texas area, SE.Q.; Knapp's Creek, near Beaudesert, at a depth of 40 feet in a well; near Roma, SE.Q.; and Lansdowne Station, near Tambo, C.Q.

SPECIFIC DIAGNOSIS: A large species, larger than *P. anak* and usually larger than *P. brehus*.

Mandible deep, with symphysis elongate, elevated to about 10° to base of mandible; lateral groove extends to below anterior root M_3 , well below alveolar margin.

I_1 elongate, very deep, markedly curved in occlusal view; enamel flanged dorso-labially, but usually unflanged and rounded ventrolingually, tip wears to produce very rounded outline. P_2 relatively elongate, with longitudinal crest high, markedly concave lingually; crest transected by broad ill-defined ridges. DP_3 with lophids high; trigonid basin narrow with broad ridge descending anteriorly into basin from metaconid; anterolabial fossette absent; weak ridge descends anteriorly from entoconid; posterior cingulum usually absent or poorly defined. P_3 relatively elongate, high, often slightly constricted at posterior one-third; crest transected by one to three sets of broad vertical labial and lingual ridges; cuspules not well defined; anterior cuspid of crest almost above anterior tooth margin. Lower molars somewhat constricted, with high lophids; trigonid basin and anterior cingulum narrow; anterolingual fossette not developed; posterior

ridge from metaconid not developed; posterior cingulum usually absent with basal posterior crown surface broadly curved in lateral view.

Upper incisors extremely broadly U-shaped in occlusal outline; I^1 extremely large; I^3 relatively small. P^3 elongate, about as long as M^4 ; markedly concave labially with marked posterolabial flexure; longitudinal crest high, markedly concave labially; crest transected anteriorly by a major set of non-vertical ridges and posteriorly by one or two minor sets; minor cuspules present; lingual cingulum sometimes discontinuous, subparallel to crest, occasionally diverging anteriorly to above paracone; cingulum not markedly tuberculate in lingual aspect. Upper molars slightly constricted across valley, with high lophs; forelink generally absent; strong anterior ridge from paracone occasionally continues to limit of cingulum; relatively strong ridge ascends posteriorly from paracone towards midlink, while slight ridge ascends anteriorly from metacone into valley; lingual limit of valley usually with prominent tuberculation.

DESCRIPTION: Mandible moderately deep, relatively thick; base of symphysis elevated at approximately 10° to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit relatively deep, near posterior symphyseal limit; diastema relatively elongate with crest posteriorly acute, more rounded anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen comparatively large, rounded, close to diastemal crest, about one-third distance along crest from P_3 to limit of ramus. Ramus with well defined, shallow, lateral groove extending posteriorly to below anterior root of M_3 , frequently disrupted by roots of P_3 ; groove positioned about one-third distance from alveolar margin to base of ramus. Diagastric process separated from base of angle by very shallow post-diagastric sulcus, bounded above by shallow diagastric fossa; this fossa separated above from shallow depression opening posteriorly into larger pterygoid fossa. Post-alveolar shelf short, with shelf angle usually not well developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of alveolar margin; masseteric foramen moderately large, with masseteric fossa relatively deep. Angle of mandible markedly inflected, flexed posteriorly at margin, broadly rounded posteriorly, ascending at high angle to posterior limit of masseteric crest. Anterior margin of coronoid process reclining at slight angle to vertical; bulk of coronoid process and condyle not preserved in adult specimens.

I_1 elongate, deeply rooted, with crown deep in unworn and juvenile specimens, slightly curved in general lateral view, markedly curved in occlusal view, developing subhorizontal facet of wear with upper incisors, and mesial facet of wear at tip by approximation with other lower incisor; root compressed oval in section; crown subquadrantal in section, somewhat tapered anteriorly, enamelled laterally, this produced into dorsolabial flange, but usually broadly rounded ventrolingually; crown also enamelled ventromesially; distally, tip wears to produce very broadly rounded anterior margin.

P_2 relatively elongate, with labial and lingual surfaces near parallel in occlusal view, converging rapidly anteriorly. Longitudinal crest secant, somewhat curved posterolingually and anterolingually, giving crest a marked lingual concavity in occlusal view; crest

transected by only broad, vertical labial and lingual ridges; anterior cuspid of crest well defined, and posterior cuspid moderately well defined. Base of crown slightly tumid.

DP₃ molariform, subtriangular in basal outline, unconstricted or slightly constricted across talonid basin, with lophids moderately high, slightly convex posteriorly. Hypolophid much broader than protolophid. Trigonid basin narrow, its length being less than distance between lophids. Forelink moderately high, strong, curving anterolingually from protoconid to point somewhat labiad to axis of crown on relatively low anterior cingulum; broad ridge descends anteriorly from metaconid into trigonid; anterolabial fossette not developed in trigonid; lingual moiety of trigonid near planar, but labial moiety descends at high angle to crown margin. Midlink moderately high, strong, curving anterolingually from hypoconid across talonid basin to unite with short, posterior ridge from near midpoint of protolophid; weak ridge descends anteriorly from entoconid. Talonid basin sharply U-shaped, near planar, descending only slightly labially and lingually from midlink. Suggestion of posterior cingulum occasionally present but very poorly defined. Base of crown occasionally tumid, particularly at margins of talonid.

TABLE 9
MANDIBULAR MEASUREMENTS FOR *Protomnodon roechus* OWEN

Specimen	P ₃	M ₁	M ₂	M ₃	M ₄
F3868 *	21.2 × 8.1	—	16.7 × —	20.0 × 12.8	—
F3397 **	18.8 × 6.5	13.1 × —	15.8 × —	17.9 × 11.9	20.0 × 12.3

* Cast of holotype *P. roechus*; ** Cast of holotype *P. antaeus*.

P₃ relatively elongate, high, morphologically simple, robust, deeply rooted; crown subovate to subtriangular in basal outline, but often very slightly constricted at posterior one-third; crest secant, moderately posterolingually curved; crest transected by one or occasionally two or three sets of broad, vertical, labial and lingual ridges, but usually without production of well defined, discrete cusps at crest. Anterior cuspid of crest almost above anterior basal limit of crown, with anterior ridge from cuspid near vertical and straight in lateral view; anterior cuspid frequently strongly defined with longitudinal crest descending sharply from it posteriorly; posterior cuspid less well defined. Base of crown tumid.

M₁ < M₂ < M₃ < M₄; molars subrectangular in basal outline, frequently somewhat constricted across talonid basin; lophids high, slightly convex posteriorly, with hypolophid broader than protolophid in M₁, approximately equal in M₂ and M₃, and slightly narrower in M₄. Trigonid basin narrow, its length approximately equalling distance between lophids. Forelink relatively high, strong, curving anterolingually from protoconid to near midpoint of low, narrow, very strongly developed anterior cingulum; this curves broadly from forelink to below protoconid, but is reduced anterolingually, and is more sharply curved lingually; trigonid basin descends at about same angle labially and lingually from forelink, but anterolingual fossette is not developed; very slight ridge descends anteriorly from metaconid, but posterior ridge into talonid basin is wanting. Midlink moderately high, strong, curving anterolingually from hypoconid to unite with

short ridge from near midpoint of protolophid, above talonid; midlink occasionally less strongly developed in posterior molars; slight ridge descends anterolabially from entoconid towards talonid; talonid basin sharply U-shaped, descending at moderate angle labially and lingually from midlink. Posterior cingulum usually absent. Base of crown usually extended posteriorly below hypolophid, frequently with basal swelling, this producing a broadly curved posterior crown surface. Lateral crown base, occasionally tumid, particularly at margin of talonid. Posterior base of crown usually marked by groove paralleling alveolar margin above limit of enamel, accompanied occasionally by minor vertical accessory ridges.

Cranium large, elongate with rostrum somewhat tapering anteriorly, only slightly deflected; maxillae dorsally in moderately wide contact with frontals; laterally with infraorbital foramen simple, above posterior of P^3 in adult specimens, positioned well in advance of jugal; infraorbital canal elongate but variable, being 39.1–43.0 ($n = 3$); inferior process of anterior zygoma root very strong, extending beyond level of occlusion of cheek teeth. Lacrymal expanded onto facial surface with lacrymal foramina on facial side of orbital rim; superior lacrymal tuberosity wide, bulbous with inferior tuberosity smaller. Premaxillae with anterior narial floor declining posteriorly, wide; anterior premaxillary narial spines very prominent; superior premaxillary surface extends posteriorly at low ascending angle, abruptly ascending above region of incisive foramen; labial foramen prominent, positioned towards margin of palate, well posterolateral to posterior rim of incisive foramen. Palate entire, penetrated posteriorly by anterior palatine foramen and posterior lateral foramen; palatines moderately large, extending anteriorly to about level of M^3 in adult specimens. Jugal laterally excavated for superficial layer of masseter, with zygomatic arches converging somewhat anteriorly, with zygomatic crest posteriorly curving backwards and ventrally. Roof of braincase arched with sagittal crest forming by confluence of ridges passing posteriorly from above orbits. Subsquamosal foramen separated below by continuation of zygomatic crest; squamosal widely separated from frontal, contributing with jugal, to glenoid fossa. External auditory meatus relatively low. Tympanic extending only slightly down paraoccipital process; processes not preserved, but bases strong. Basisphenoid only slightly grooved posteriorly at mid-line. Pterygoids slightly overlap basisphenoid, being in sutural contact. Supraoccipital relatively low, wide, with lambdoidal crest extending posteriorly to marked extent with well defined supraoccipital depressions separated by moderate, rounded, median nuchal crest; inferior supraoccipital depressions absent. Condylod foramen prominent. Dorsal surface with nasal–frontal suture approximately level with anterior orbital rim. Nasals very retracted.

Upper incisors extremely broadly U-shaped in occlusal outline; I^1 extremely large compared with I^2 and I^3 , axially curved; directed anteroventrally and somewhat mesially with tips approximated; labial surface curved towards occlusal surface but becoming grooved at posterior one-third towards limit of enamel; enamel surface extends anteromesially and posteromesially but does not reach lingual surface of crown; anterolateral, posterolateral and posteromesial margins of crown sharply rounded, but anteromesial margin broadly rounded; occlusal surface becomes nearly horizontal with wear, with slight projection of enamel where present, resulting in large area for occlusion. I^2 not

sufficiently well preserved to be described. I^3 relatively small, short in anteroposterior extent, not known in unworn condition; lateral surface marked by vertical groove about one-half way along its occlusal surface, this extending towards crown base; enamel present on all surfaces of crown; wear predominantly mesiad, with production of high angle wear facet ascending mesially.

No upper canine has yet been located, and P^2 and DP^3 are unknown.

P^3 elongate, being approximately as long as longest molar, slightly broader posteriorly than anteriorly; crown in occlusal view subcrescentic, markedly concave labially, with a marked posterolabial flexure, but nearly straight or slightly concave lingually; longitudinal crest secant, but also markedly posterolabially curved, moderately high; apex of paracone about one-fifth distance along crown from anterior point; anterior ridge from paracone frequently stronger, developed basally and curving lingually; crest transected anteriorly by major set of non-vertical labial and lingual ridges, and posteriorly by one or two minor sets of ridges; cuspules produced at crest, decreasing in development posteriorly. Hypocone moderately high, being about three-quarters as high as metacone, united to above metacone by strong, high, labial ridge; posterior ridge from metacone ascends towards crown base; posterior ridge from hypocone curves labially to above metacone; well defined posterior fossette developed between this and ridge connecting posterior cusps. Anterior ridge from hypocone ascends sharply to form low, frequently discontinuous anteriorly, lingual cingulum, generally subparalleling crest anteriorly, but occasionally slightly diverging anteriorly to above paracone, connected to it by moderately strong ridge. Ridges from cuspules along crest cross lingual basin to cingulum; antero-lingual fossette occasionally formed particularly where cingulum discontinuous. In lingual aspect, cingulum not markedly tuberculate. Base of crown often markedly tumid.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, very slightly constricted across median valley; lophs moderately high, slightly bowed anteriorly; metaloph slightly broader than protoloph in M^1 , approximately equal in M^2 and M^3 and somewhat narrower in M^4 . Anterior cingulum low, relatively broad, short, nearly planar transversely; generally no trace of distinct forelink present, but occasional variable ridgelets pass from base of protoloph to cingulum; anterior margin of cingulum generally flattened. Moderately strong ridge ascends from paracone towards labial limit of cingulum, occasionally continued from base of protoloph across cingulum margin. Strong ridge usually ascends posterolingually from paracone towards midlink. Midlink moderately strong and high, curving posterolabially from protocone to unite with short ridge from near mid-point of metaloph, above median valley; relatively strong ridge curves posterolingually from paracone towards midlink; slight ridge from metacone ascends anterolingually into median valley. Median valley narrowly U-shaped labially, more broadly U-shaped lingually; base of valley near planar transversely; lingual limit of valley usually marked by prominent tuberculation. Strong, slightly flared ridge curves posterolabially from hypocone to base of crown slightly mesiad to posterolabial limit, uniting with weaker ridge ascending slightly posterolingually from metacone. Slight posterior fossette formed between ridges and base of metaloph, labiad to crown axis.

DISCUSSION: Material referred to *Protemnodon roechus* Owen is moderately common in the Pleistocene fluvial deposits of the Darling Downs and is recorded from isolated

TABLE 10
SUMMARY OF MEASUREMENTS FOR *Protemnodon roechus* OWEN

Character	Maxillae					Mandibles				
	n	O.R.	\bar{X}	s	V	n	O.R.	\bar{X}	s	V
I ₁ depth	—	—	—	—	—	2	17.9-18.2	18.1	—	—
P ₂ length	—	—	—	—	—	2	11.9	11.9	—	—
Maximum breadth ..	—	—	—	—	—	2	6.2-6.3	6.3	—	—
DP ₃ length	—	—	—	—	—	3	11.6-11.9	11.7	0.1599	1.37
Breadth protolophid ..	—	—	—	—	—	3	6.8-7.4	7.2	0.3240	4.50
P ₃ length	—	—	—	—	—	11	17.5-21.2	18.8	0.9121	4.85
Maximum breadth ..	7	18.3-20.7	19.4	0.7538	3.89	13	6.0-8.1	7.0	0.5852	8.36
M ₁ ¹ length	7	9.2-10.4	9.7	0.4337	4.47	12	12.4-14.2	13.3	0.6612	4.97
Breadth protoloph (-id) ..	4	12.9-14.0	13.4	0.5567	4.15	8	8.9-9.9	9.4	0.3761	4.00
M ₂ ² length	9	12.2-13.9	12.8	0.5926	4.63	22	14.0-18.0	16.1	0.9332	5.80
Breadth protoloph (-id) ..	12	15.7-17.7	16.7	0.6037	3.61	11	10.6-12.2	11.3	0.5147	4.55
Height*	10	13.7-15.4	14.6	0.5217	3.57	1	10.5	—	—	—
M ₃ ³ length	2	12.2-12.5	12.4	—	—	28	16.8-20.3	18.5	0.9704	5.25
Breadth protoloph (-id) ..	18	17.2-19.9	18.6	0.8311	4.47	31	11.2-13.6	12.5	0.5193	4.15
Height*	12	14.9-16.2	15.6	0.3512	2.25	10	7.9-10.6	9.7	0.7370	7.60
M ₄ ⁴ length	3	12.4-13.2	12.8	—	—	24	17.3-20.9	19.7	0.6896	3.50
Breadth protoloph (-id) ..	13	17.7-20.0	19.0	0.7900	4.16	22	11.1-13.8	12.6	0.6015	4.77
Height*	11	14.7-16.5	15.7	0.5531	3.52	13	8.3-10.0	9.2	0.5074	5.52
	7	9.9-13.1	11.5	1.1075	9.63					

* Enamel height measured at hypocone and entoconid in unworn teeth.

localities from other parts of Queensland, but it is not nearly as well represented in collections as the smaller species, *P. anak*. The species was described by Owen (1874) and includes the largest representatives of the genus yet known. Slightly smaller representatives, previously referred to the species *P. antaeus*, described by Owen (1877), cannot be separated from *P. roechus* by either size or structure where the sample is sufficiently large for variation to be taken into account. The holotype of *P. antaeus* is morphologically very similar to *P. roechus* and the two are here regarded as synonymous. Measurements for the holotype specimens are presented in Table 9.

Association of upper and lower dentigenous fragments of *P. roechus* has been achieved through a combined consideration of both size and morphology. No attempt has been made to associate any of the post-cranial material in the Queensland Museum collections with the described cranial remains because of the disarticulated and fragmentary nature of the specimens at present known.

The accompanying summary of measurements, Table 10, presents statistical evaluation of the population of *P. roechus* represented in the holdings of the Queensland Museum and includes both mandibular and maxillary specimens. The generally low values for the Coefficient of Variation are in keeping with values for other species of *Protemnodon* here considered and with other fossil and recent macropodids (Bartholomai, 1971). As with other species of *Protemnodon* values for V for height of enamel are moderately high compared with other characters considered and for reasons presented for other species, discussed above, are not indicative of real variation in the height of the crown. The sample of *P. roechus* presents only very limited numbers of specimens possessing certain of the characters considered and, in these cases, the statistical results represent no more than a guide to the range of variation exhibited in the local population.

An indication of the variation present in the premolar teeth is illustrated in Figure 7, while measurements for the referred upper incisor teeth are shown in Table 11.

P. roechus is distinguished from other known species of *Protemnodon* by both its extreme size and generally distinct morphology. In particular, the relatively less ornamented nature of its permanent lower premolar, the broadly rounded, swollen condition of the posterior crown bases of the lower molars, the non-vertical transecting ridges of the permanent upper premolars, the crescentic shape of this tooth in occlusal view and the generally marked tuberculation of the lingual extremity of the median valley in upper molars are all useful in the morphological separation of the species. Overlap in size does occur with *P. brehus*, but by applying a combination of the characters available, separation of the species is achieved.

Several mandibular specimens from the Pleistocene fluviatile deposits are present whose taxonomic position has not been able to be satisfactorily resolved and these are referred doubtfully to the present species, but have not been considered statistically in this study. These include F5082 and F3039, both of which are within the size range of *P. roechus* and have generally similar morphology to the referred material, but have a well developed posterior cingulum. F5084, also included in this doubtfully referred material, is morphologically identical to *P. roechus* but is much smaller, within the size range of *P. anak* specimens.

A very small sample of mandibular remains of *P. roechus* derived from the Pleistocene fluviatile deposits at Bingara, New South Wales, is present in material made available from the Australian Museum, Sydney. Variation in this sample is entirely encompassed by that seen in the Darling Downs material. Measurements for the Bingara sample are presented in Table 12.

TABLE 11
MEASUREMENTS FOR UPPER INCISORS IN *Protemnodon roechus* OWEN

Specimen	F5053	F5295	F5284	F5294	F5291
Length I ¹ ..	16.1	17.0	15.3	14.8*	15.2
Length I ³ ..	8.0*	—	—	—	—

* Estimated

Apart from the localities already noted, *P. roechus* has not been as widely mentioned in literature as other Pleistocene species. Tindale (1933) has recorded it from the Tantanoola Caves in the southeast of South Australia but the record is not accompanied by either a description or figure and the identity of the specimen must at present remain in doubt. Specimens exist in the Australian Museum, Sydney, which are undoubtedly of *P. roechus* and which were derived from the Wellington Caves. Within these, there is a tendency towards narrowing of the anterior cingulum and trigonid basin, an extreme of which is present in AM F30524, a right ramus with M₂–M₄ preserved.

TABLE 12
MANDIBULAR MEASUREMENTS FOR *Protemnodon roechus* OWEN—BINGARA SAMPLE

Specimen	M ₂	M ₃	M ₄
AM MF1233 ..	—	18.0 × 12.0	19.0 × 12.1
AM MF1221 ..	—	—	19.7 × 13.2
AM MF1157 ..	16.1 × —	17.9 × 12.1	19.4 × 12.6

***Protemnodon chinchillaensis* sp. nov.**

(Plates 20–21)

Protemnodon anak Owen: De Vis. 1895 (*partim*), pp. 104–109.

MATERIAL: F5246, holotype, partial right mandibular ramus with M₂–M₄, adult, Chinchilla Sand of late Pliocene age, Chinchilla, SE.Q. This specimen has been associated with the anterior portion of a right mandibular ramus with P₃, previously numbered F5238.

Eight juvenile mandibular rami, 19 adult mandibular rami, 1 isolated lower tooth, 2 juvenile maxillae, 11 adult maxillae and 5 isolated upper teeth from the following localities in the Chinchilla Sand, in the western Darling Downs: Chinchilla, SE.Q.; Middle Gully System, Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla), 55 feet above low water level; and from the western Darling Downs (particular localities unspecified).

SPECIFIC DIAGNOSIS: A small species, generally somewhat smaller than *P. anak*.

Mandible comparatively very shallow, with symphysis relatively elongate, ascending at about 5° to base of mandible; lateral groove extends posteriorly to below anterior root M_3 , well below alveolar margin; mental foramen close to anterior root P_3 .

P_2 elongate, relatively low crowned, with crest slightly curved lingually in its posterior extension; crest transected by two or three sets of vertical labial and lingual ridges; cuspules present. DP_3 slightly constricted across talonid basin, with low lophids; protolophid very convex posteriorly; trigonid basin relatively narrow; forelink slightly curved; strong, angular ridge descends from metaconid to lingual limit of high anterior cingulum, across swollen base of protolophid; anterolabial fossette present; lingual moiety of trigonid pocket-like; midlink relatively strong; weak ridges from metaconid and entoconid unite across talonid; posterior cingulum well defined. P_3 very elongate, much longer than M_4 , constricted at posterior one-third; crest low, usually straight, transected by four or five sets of vertical labial and lingual ridges; cuspules present. Lower molars slightly to markedly constricted across talonid basin, with lophids low, forelink labiad to midline; slight ridge descends anteriorly from metaconid; base of protolophid swollen lingually; midlink labiad to mid-line; slight ridges from metaconid and entoconid often unite across talonid, close to midlink, talonid broadly U-shaped; posterior cingulum usually well defined, broad.

DP^3 with midlink paralleled labially by low ridge across valley. P^3 very elongate, much longer than M^4 , with longitudinal crest low, nearly straight; crest transected by four or five sets of vertical labial and lingual ridges, cuspules present; lingual cingulum often continues anteriorly to near anterior of crown base; cingulum markedly sinuous and tuberculate in lingual view. Upper molars with low lophs, unconstricted or slightly constricted across valley of anterior molars but more constricted posteriorly; strong, high, ridge usually ascends from paracone to limit of cingulum, but this sometimes reduced in M^4 ; midlink relatively low; strong ridges from paracone and metacone normally unite across median valley giving impression of additional low link.

DESCRIPTION: Mandible very shallow, relatively thick; base of symphysis ascending anteriorly at an angle of approximately 5° to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit relatively shallow, near posterior symphyseal limit; diastema elongate, with diastemal crest broadly angular posteriorly, more rounded anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen small, oval, near diastemal crest, close to anterior root P_3 . Ramus with moderately deep lateral groove extending posteriorly to below anterior root M_3 , usually somewhat disrupted by roots of P_3 ; groove positioned well below alveolar margin, about one-third depth of ramus below alveolar margin. Diagastric process separated from base of angle by very shallow post-diagastric sulcus, bounded above by shallow diagastric fossa; this fossa separated above from shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf moderately short, with well defined shelf angle usually not developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of alveolar margin; masseteric

foramen moderately large, with deep masseteric fossa. Angle of mandible, bulk of coronoid process and condyle not preserved.

I_1 not preserved.

P_2 relatively elongate, subovate in occlusal view, with lingual surface slightly convex and labial surface markedly convex. Longitudinal crest secant, slightly curving lingually in its posterior extension; anterior ridge from anterior cuspid slightly curved lingually and strengthening towards base of crown; crest transected by two or three sets of vertical labial and lingual ridges, with production of cuspules at crest; ridges and cuspules progressively weaken posteriorly; anterior cuspid of crest well defined, but posterior cuspid less well developed. Base of crown somewhat tumid.

DP_3 molariform, subtriangular in basal outline, slightly constricted across talonid basin, with lophids relatively low, with hypolophid slightly convex posteriorly and with protolophid very convex posteriorly; hypolophid much broader than protolophid. Trigonid basin relatively narrow, its length being less than distance between lophids. Forelink moderately high, strong, very slightly curving anterolingually or straight from protoconid to near midpoint of moderately high anterior cingulum; strong angular ridge descends anteriorly from metaconid to lingual limit of anterior cingulum, across swollen base of protolophid; labially, cingulum unites with protolophid base with production of slight anterolabial fossette; lingual portion of trigonid base pocket-like, near horizontal, but labial moiety descends at high angle. Midlink relatively strong, curving anterolingually from hypocone across talonid basin to unite with slight ridge from near midpoint of protolophid; weak ridge descends posteriorly from metaconid across lingual moiety of talonid to unite with weak anterior ridge from entoconid. Talonid basin sharply U-shaped, descending at greater angle labially than lingually from midlink. Posterior cingulum well defined, near horizontal with very slight ridge ascending at posterolingual margin of crown to entoconid. Base of crown slightly tumid, particularly at labial extremity of talonid basin.

P_3 comparatively very elongate, robust, deeply rooted; crown subovate to dumbbell shaped in basal outline, slightly to strongly constricted at posterior one-third, with longitudinal crest secant, straight or very slightly concave lingually except for lingual flexure in its posterior extension; crest usually transected by five sets of vertical labial and lingual ridges with production of cuspules at crest, but occasionally four sets of ridges and resultant cuspules present; strength of ridges and cuspules decreases posteriorly; anterior cuspid of crest well defined, but posterior cuspid less well developed; base of crown slightly tumid.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly to markedly constricted across talonid basin; lophids relatively low, slightly convex posteriorly, with hypolophid broader than protolophid in M_1 , approximately equal in M_2 and M_3 and narrower in M_4 . Trigonid basin relatively broad, its length approximately equalling distance between lophids. Forelink moderately low, relatively strong, curving anterolingually from protoconid across trigonid to point on anterior cingulum labial to midline. Anterior cingulum low, generally broadly curved anteriorly, near horizontal lingually but descending slightly labially; slight ridge descends anteriorly from metaconid; base of protolophid swollen in lingual moiety, very occasionally with suggestion of presence of

accessory vertical ridge. Midlink moderately low, moderately strong but usually decreasing in strength in posterior molars, curving anterolingually from hypoconid to unite with slight ridge from protolophid from point labiad to midline; slight ridge descends posterolabially from metaconid and frequently unites across talonid, close to midlink, with slight anterolabial ridge from entoconid. Talonid basin broadly U-shaped, descending at low angle labially and lingually from midlink; occasionally, labial moiety ornamented with low, transverse ridge. Posterior cingulum usually well defined, frequently extending across entire posterior of crown, occasionally united by slight ridge to entoconid.

Cranium known only from fragmentary maxillary remains.

Upper incisors unknown, and P^2 known only in very fragmentary state.

DP^3 preserved only in worn and partially shattered condition; molariform, subrectangular in basal outline, with low lophs; paracone not preserved; anterior cingulum connected to base of protoloph by slight ridges near axis of crown; midlink moderately strong, paralleled labially by low ridge across median valley uniting paracone and metacone. Strong ridge curves posterolabially from hypocone to above metacone; weaker ridge ascends slightly lingually from metacone to unite with this, defining posterior margin to posterior fossette.

P^3 relatively very elongate, being much longer than any molar, somewhat broader posteriorly than anteriorly; crown with longitudinal crest secant, relatively low, usually nearly straight except in posterior extension where crest is slightly labially flexed; apex of paracone about one-fifth distance along crown from anterior limit; crest transected by five or sometimes four sets of vertical labial and lingual ridges, with production of cusps at crest; strength of ridges and cusps decreases posteriorly. Hypocone moderately high, being about three-quarters as high as metacone, united to above metacone by strong, high, labial ridge; strong ridge from hypocone ascends posterolabially to unite with posterior ridge from metacone; well defined posterior fossette developed between this and ridge connecting posterior cusps. Anterior ridge from hypocone ascends sharply to form low lingual cingulum, generally converging anteriorly to above paracone, connected to it by moderately strong vertical ridge; slight extension of lingual cingulum occasionally ascends beyond this point to anterolingual base of crown; more prominent ridges from cusps along longitudinal crest cross shallow lingual basin to lingual cingulum; cingulum markedly sinuous and tuberculate in lingual aspect. Base of crown somewhat tumid.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, unconstricted or slightly constricted across median valley in anterior molars, frequently more so in M^4 ; lophs relatively low, slightly bowed anteriorly, with metaloph broader than protoloph in M^1 , approximately equal in M^2 , slightly narrower in M^3 and usually markedly narrower in M^4 . Anterior cingulum low, broad and short, slightly descending labially; generally no trace of a distinct forelink present; variable slight ridges usually pass from base of protoloph towards cingulum; cingulum generally broadly rounded anteriorly. Strong, high ridge ascends anteriorly from paracone to labial limit of cingulum, but this is sometimes reduced in M^4 . Midlink relatively low, usually moderately strong in anterior molars but quite weak in some posterior molars, curving posterolabially from protocone to unite with slight ridge from near midpoint of metaloph, above median valley; in anterior

TABLE 13
SUMMARY OF MEASUREMENTS FOR *Protemnodon chinchillaensis* SP. NOV.

Character	Maxillae					Mandibles				
	n	O.R.	\bar{X}	s	V	n	O.R.	\bar{X}	s	V
P ₂ length	—	—	—	—	—	2	9.6-11.1	10.4	—	—
Maximum breadth ..	—	—	—	—	—	2	4.5- 5.5	5.0	—	—
DP ₃ length	2	10.2-10.7	10.5	—	—	4	9.6- 9.9	9.7	0.1288	1.33
Breadth protolophid ..	—	—	—	—	—	4	5.7- 6.4	6.0	0.3414	5.69
P ₃ length	1	19.5	19.5	—	—	9	15.7-17.9	17.1	0.6117	3.58
Maximum breadth ..	4	8.2- 9.2	8.7	0.4242	4.88	9	4.9- 6.2	5.5	0.3674	6.68
M ₁ length	4	10.4-11.6	11.0	0.4967	4.52	8	9.9-11.4	10.6	0.6939	6.55
Breadth protoloph (-id) ..	5	9.3-11.3	10.3	0.7314	7.10	7	7.8- 8.3	8.0	0.1958	2.45
M ₂ length	7	11.7-13.4	12.5	0.5400	4.32	15	10.9-12.8	12.1	0.5977	4.94
Breadth protoloph (-id) ..	9	10.5-12.6	11.7	0.6072	5.19	15	8.6- 9.5	9.1	0.2718	2.99
Height*	2	8.1-10.4	9.3	—	—	6	6.4- 7.4	6.8	0.3847	5.66
M ₃ length	6	13.3-14.7	14.2	0.5603	3.95	15	12.7-14.8	13.6	0.5856	4.31
Breadth protoloph (-id) ..	6	11.6-12.9	12.3	0.5933	4.82	15	9.5-10.9	9.9	0.3769	3.81
Height*	3	7.3- 8.8	7.9	—	—	9	6.3- 7.7	6.9	0.4885	7.08
M ₄ length	12	13.7-14.8	14.3	0.4400	3.08	8	13.5-14.6	14.1	0.4140	2.94
Breadth protoloph (-id) ..	11	10.7-13.0	12.1	0.7183	5.94	8	9.2-10.1	9.7	0.3184	3.28
Height*	11	6.6- 9.0	7.7	0.5857	7.61	7	6.0- 7.5	6.6	0.4812	7.29

* Enamel height measured at hypocone and entoconid in unworn teeth.

TABLE 14
MANDIBULAR MEASUREMENTS FOR *Protemnodon chinchillaensis* SP. NOV.

Specimen	P ₃	M ₁	M ₂	M ₃	M ₄
F5246 * ..	17.6 × 5.9	—	10.9 × 8.8	13.5 × 9.8	14.6 × 9.2

* Holotype *P. chinchillaensis*

molars and to some extent in posterior molars, strong ridge ascends posterolingually from paracone usually to unite with equally strong ridge ascending anterolingually from metacone across median valley about one-half way between midlink and labial margin; this frequently gives crown the appearance of possessing lateral links. Median valley narrowly V-shaped labially and lingually; base of valley not markedly ascending labially or lingually from midlink. Strong, slightly flared ridge ascends posterolabially from hypocone to posterolabial base of crown, uniting with lesser ridge from metacone; this delimits posterior fossette slightly labiad to crown axis.

DISCUSSION: Most of the material here referred to *P. chinchillaensis* sp. nov. was included in that referred by De Vis (1895) to *Halmaturus anak*. De Vis's (1895) concept of the specific limits within the genus was extremely broad, and he stated that he could not determine any criteria by which separation could be achieved. It was, however, acknowledged that the variation exhibited by the combined sample was high.

It has now been widely illustrated that an age difference occurs within the Darling Downs samples, and that this is frequently indicated by specific and even generic differences between material from the Pleistocene fluvial deposits and that from the Chinchilla Sand (Bartholomai, 1972).

P. chinchillaensis is the smallest species of *Protemnodon* yet recorded from Australia, and is morphologically distinct from other Pliocene and Pleistocene species. It is slightly larger than the small Pliocene New Guinea species, *P. buloloensis* Plane. Major morphological features distinguishing it from species from the Pleistocene fluvial deposits include the low crown heights of the cheek teeth, the relatively more elongate permanent premolars compared with molar lengths, the relative strength of molar accessory ridging and the moderately weak midlinks, and the shallow depth of the mandibular ramus.

Its distinction from the other Chinchilla Sand species, *P. devisi* sp. nov. described below, is by both size and morphology. In particular, *P. chinchillaensis* is smaller, and has the mandibular ramus shallower, while the permanent premolars are comparatively longer, the links are more curved in the molars, and the anterolingual base of the protolophid is swollen. The comparatively more elongate nature of the permanent lower premolar also serves to separate *P. chinchillaensis* from *P. buloloensis*.

As seen in the accompanying summary of maxillary and mandibular measurements, outlined in Table 13, the sample is not large, and many of the characters are too inadequately represented to allow all but the broadest generalities on the population to be drawn. Values for the Coefficient of Variation are comparable with those for other species of *Protemnodon*, and are generally not excessive. The occasional, extremely low values for V are believed to relate to the small size of the sample. Measurements for the holotype

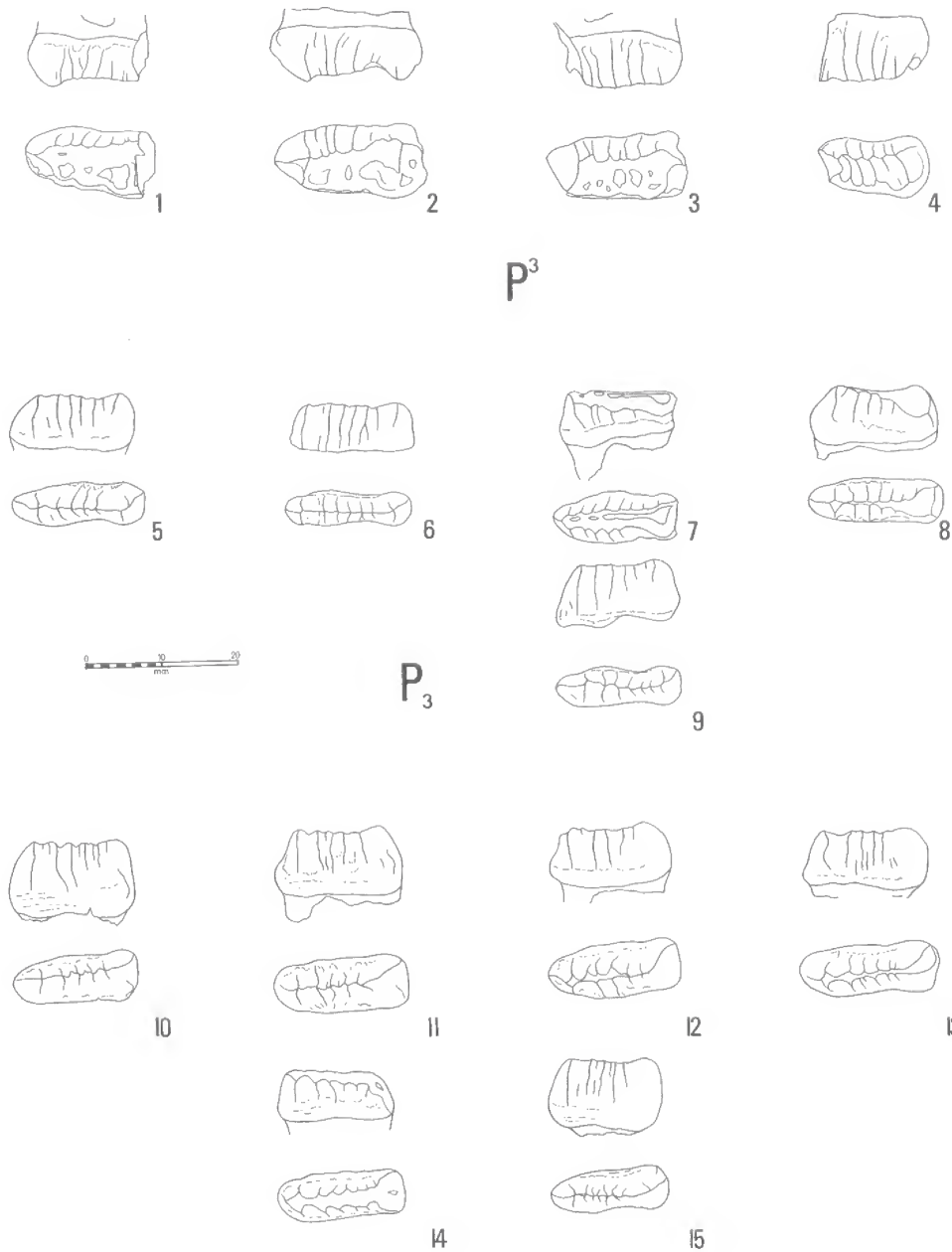


FIG. 8: Morphological variation in the permanent premolar teeth in *Protamnodon chinchillaensis* sp. nov. (1–9) and *Protamnodon devisi* sp. nov. (10–15). Lateral view above, occlusal view below. 1, right P^3 reversed, F5244; 2, left P^3 , F4719; 3, right P^3 reversed, F4727; 4, right P^3 reversed, F5243; 5, left P_3 , F3676; 6, left P_3 , F5242; 7, left P_3 , F5299; 8, right P_3 reversed, F5246; 9, right P_3 reversed, F4813; 10, right P_3 reversed, F4720; 11, right P_3 reversed, F3042; 12, left P_3 , F4709; 13, left P_3 , F4664; 14, left P_3 , F4710; 15, left P_3 , F4807.

specimen, F5246, are listed in Table 14, while variation in morphology in premolar teeth is illustrated in Figure 8.

General morphological resemblances of the species are with *P. anak* rather than with any other of the Pleistocene species, but at this stage too little is known of *P. chinchillaensis* for any definite relationships to be suggested.

***Protemnodon devisi* sp. nov.**

(Plates 22–3)

Protemnodon anak Owen: De Vis, 1895 (*partim*), pp. 104–109.

MATERIAL: F4710, holotype, partial left mandibular ramus with P_3 , M_2 – M_4 , adult, Chinchilla Sand of late Pliocene age, Chinchilla, SE.Q. This specimen has been reassociated with the anterior portion of a left mandibular ramus with P_3 , previously numbered F4671.

Nine juvenile mandibular rami, 35 adult mandibular rami, 5 isolated lower teeth, 2 juvenile maxillae, 9 adult maxillae and 4 isolated upper teeth, from the following localities in the late Pliocene Chinchilla Sand, in the western Darling Downs: Chinchilla, SE.Q.; near Condamine River, gully in eastern part of por. 270, Par. Chinchilla; ?Chinchilla; near M.R. 362676 Chinchilla 4 mile map; well at Ehlma Siding, about 60' below surface; and from the western Darling Downs (particular localities unspecified).

SPECIFIC DIAGNOSIS: A medium-sized *Protemnodon*, generally somewhat larger than *P. anak*.

Mandible moderately shallow, with symphysis elongate, elevated at about 15° to base of mandible; lateral groove extends posteriorly to below M_2 – M_3 .

P_2 relatively elongate, with crest low, slightly convex labially, transected by two sets of vertical labial and lingual ridges; cuspules present. DP_3 unconstricted across talonid, with lophids low; forelink labiad to axis of crown; anterolabial fossette present in trigonid; midlink labiad to axis; moderate ridge descends anteriorly from entoconid into talonid; broad, well defined posterior cingulum present. P_3 relatively elongate, with longitudinal crest moderately high, crown somewhat constricted at posterior one-third; crest nearly straight, transected by three or four sets of vertical labial and lingual ridges; cuspules present. Lower molars slightly constricted across talonid, with lophids low; trigonid very broad, near planar transversely; anterolabial fossette slight; forelink only slightly curved, as is midlink; midlink relatively low; slight ridge occasionally descends anteriorly from entoconid into talonid; posterior cingulum broad.

P^2 elongate, considerably broader posteriorly than anteriorly; lingual crest moderately low, slightly concave labially, transected by two sets of vertical labial and lingual ridges; cuspules present; third lingual ridge present posteriorly; lingual cingulum continues to above paracone; cingulum sinuous and tuberculate in lingual view. DP^3 slightly constricted across median valley; lophs low; anterior cingulum broad; strong ridge ascends from paracone to labial limit of cingulum; midlink relatively low, only slightly curved; relatively strong ridges from paracone and metacone unite across median valley. P^3 elongate, with longitudinal crest low, nearly straight; crest transected by four sets of vertical labial and lingual ridges; cuspules present; lingual cingulum continues anteriorly to near anterior crown limit; cingulum very irregularly sinuous in lingual view. Upper

TABLE 15
SUMMARY OF MEASUREMENTS FOR *Protemnodon devisi* SP. NOV.

Character	Maxilla					Mandible				
	n	O.R.	\bar{X}	s	V	n	O.R.	\bar{X}	s	V
P ₂ length	1	13.8	13.8	—	—	2	9.6-10.4	10.0	—	—
Maximum breadth	1	7.9	7.9	—	—	2	5.0- 5.3	5.2	—	—
DP ₃ length	1	12.0	12.0	—	—	2	9.7- 9.8	9.8	—	—
Breadth protoloph (-id)	1	9.4	9.4	—	—	2	5.7- 6.0	5.9	—	—
P ₃ length	2	19.4-19.6	19.5	—	—	9	15.8-17.5	16.7	0.6633	3.97
Maximum breadth	2	9.3-10.4	9.8	—	—	12	5.5- 7.5	6.5	0.6522	10.03
M ₁ length	4	12.2-13.2	12.6	0.4202	3.33	8	10.8-12.2	11.5	0.4225	3.67
Breadth protoloph (-id)	4	10.4-12.0	11.4	0.7164	6.28	9	7.9- 8.9	8.4	0.3201	3.81
M ₂ length	7	13.7-15.6	14.6	0.7234	4.95	22	11.8-15.5	13.9	0.8978	6.46
Breadth protoloph (-id)	6	12.5-13.8	13.2	0.4604	3.49	21	9.1-11.1	10.0	0.4577	4.58
Height*	4	8.9-11.7	10.8	1.2832	11.88	10	6.3- 8.2	7.6	0.6624	8.72
M ₃ length	8	14.3-16.6	15.7	0.7679	4.89	23	14.8-16.9	15.9	0.4981	3.13
Breadth protoloph (-id)	8	12.5-14.0	13.2	0.5428	4.11	24	10.3-12.0	11.3	0.4759	4.21
Height*	4	11.0-11.8	11.5	0.3558	3.09	9	6.7- 8.7	7.7	0.6412	8.33
M ₄ length	3	16.2-17.1	16.5	—	—	14	15.5-17.9	16.5	0.6462	3.92
Breadth protoloph (-id)	3	13.4-13.8	13.6	—	—	17	10.5-12.0	11.2	0.5055	4.51
Height*	2	8.2-10.1	9.2	—	—	7	6.4- 8.6	7.3	0.7659	10.49

* Enamel height measured at hypocone and entoconid in unworn teeth.

molars very slightly constricted across median valley, with lophs low; relatively strong ridge ascends from paracone to labial limit of cingulum; midlink moderately low, very slightly curved; strong ridge from metacone across median valley; lingual limit of valley occasionally tuberculate.

DESCRIPTION: Mandible relatively shallow and thick; base of symphysis elevated at approximately 15° to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit relatively deep, near posterior symphyseal limit; diastema relatively elongate with crest posteriorly acute, becoming more broadly rounded anteriorly; ventral margin of ramus rounded between symphysis and extremely weak diagastric ridge and process. Mental foramen relatively large, rounded, usually well below diastemal crest but sometimes close to crest. Ramus with well defined, shallow, lateral groove extending posteriorly to below M_2-M_3 , often disrupted by roots of P_3 ; groove positioned about one-third distance from alveolar margin to base of ramus. Diagastric process bounded above by diagastric fossa; this fossa separated above from very shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, with shelf angle usually not well developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process. Coronoid process, condyle and angle of mandible not preserved in any specimen.

I_1 not preserved.

P_2 relatively elongate, very slightly broader posteriorly than anteriorly. Longitudinal crest secant, slightly convex labially, more flexed lingually in its posterior extension; slight fossette formed posterior to posterior cuspid. Crest transected by two sets of vertical labial and lingual ridges with production of cuspules at crest; strength of ridges and cuspules decreases posteriorly. Anterior cuspid of crest well defined. Base of crown tumid.

DP_3 molariform, subtriangular in occlusal view, unconstricted across talonid basin, with protolophid much narrower than hypolophid. Trigonid basin very broad, elongate. Forelink well defined, extending anteriorly to point on anterior cingulum labial to axis of crown; anterior cingulum relatively low; slight fossette present in labial moiety of trigonid. Midlink moderately strong, curving anterolingually from hypoconid to point on protolophid labial to crown axis; talonid basin shallowly U-shaped in labial and lingual moieties; moderate ridge descends anterolabially from entoconid across talonid about one-half way between midlink and lingual margin; labially, talonid margin somewhat tumid. Moderate ridge descends posteriorly from entoconid to unite with lingual limit of broad, well defined posterior cingulum, nearly as broad as posterior base of hypolophid.

P_3 relatively elongate, moderately high, robust, deeply rooted; crown subovate in occlusal view, usually broadest mesially, somewhat constricted basally at posterior one-third. Crest secant, nearly straight, usually being only very slightly convex labially; posterior extension slightly more flexed lingually; crest transected by three and sometimes four sets of vertical labial and lingual ridges with production of cuspules at crest; strength of ridges and cuspules decreases posteriorly. Anterior ridge from anterior cuspid descends at moderate angle to crown base. Base of crown slightly tumid.

TABLE 16
MANDIBULAR MEASUREMENTS FOR *Protemnodon devisi* SP. NOV.

Specimen	P ₃	M ₁	M ₂	M ₃	M ₄
F4710 *	— × 5.8	—	—	15.1 × 10.5	15.6 × 10.6
AM F15464	—	—	14.0 × 10.5	16.0 × 11.5	16.8 × 11.4

* Holotype *P. devisi* sp. nov.

M₁ < M₂ < M₃ < M₄; molars subrectangular in basal outline, slightly constricted across talonid basin; lophids relatively low, slightly convex posteriorly, with hypolophid broader than protolophid in M₁ and M₂, approximately equal in M₃ and somewhat narrower in M₄. Trigonid basin very broad, elongate, its length approximately equalling distance between lophids. Forelink relatively high, moderately strong, slightly curving anterolingually from protoconid to near midpoint of low, very broad, anterior cingulum; cingulum broadly curved labially and lingually from forelink to base of protolophid; trigonid basin near planar transversely, often with slight anterolabial fossette formed at margin of labial moiety; anterior ridge from metaconid usually absent, often replaced by slight groove. Midlink relatively weak, moderately low, slightly curving anterolingually from hypoconid to point labiad to crown axis on protolophid; very slight ridge occasionally present descending anterolabially from entoconid towards talonid basin; basin sharply U-shaped labially and lingually, descending at approximately same angle from midlink, in both moieties. Slight posterior ridge from entoconid descends to unite with lingual extremity of posterior cingulum; occasionally, slight ridge also present from hypoconid, descending to labial margin of cingulum; cingulum broad, well defined.

Cranium known only from extremely fragmentary maxillary remains.

Upper incisors unknown.

P² elongate, robust, subtriangular in basal outline, considerably broader posteriorly than anteriorly; longitudinal crest moderately low, secant, slightly concave labially; crest transected by two sets of vertical labial and lingual ridges with production of cuspules at crest; posteriorly, a third lingual ridge descends to crest; apex of paracone positioned about one-quarter length of crown from anterior limit. Hypocone moderately strong, united to metacone by strong, high, descending anterolabial ridge; posterior ridge from hypocone curves labially, ascending slightly towards crown base above metacone, uniting with posterior extension of longitudinal crest from metacone; well defined posterior fossette formed between this and ridge connecting cusps; anterior ridge from hypocone ascends rapidly to above crown base to form low lingual cingulum, converging markedly anteriorly to above paracone; paracone connected to cingulum by moderately strong lingual ridge; cingulum in lingual view markedly sinuous, tuberculate. Lingual basin shallow, subdivided into well defined pockets by extensions of ridges from cuspules at longitudinal crest to cingulum. Base of crown slightly tumid labially and anterolingually.

DP₃ molariform, subtriangular in basal outline, slightly constricted across median valley. Lophs moderately low, slightly convex anteriorly, with metaloph broader than protoloph. Anterior cingulum low, broad, short, near planar transversely; several

moderately strong ridgelets pass from base of protoloph to anterior cingulum, but distinct forelink not developed; cingulum flattened anteriorly, with strong ridge descending from labial margin to paracone; slight anterolingual fossette present at lingual limit of cingulum. Midlink relatively strong, moderately low, slightly curving posterolabially from protocone to unite with slight ridge from near midpoint of metaloph; relatively strong ridge curves posterolingually from paracone to unite with similar ridge from metacone across median valley, about one-half way between midlink and labial margin. Median valley sharply U-shaped, near planar transversely. Strong, slightly flared ridge curves posterolabially from hypocone to above metacone, uniting with lesser ridge from that cusp. Posterior fossette delimited by these ridges, positioned slightly labiad to crown axis.

P³ elongate, subtriangular in basal outline, somewhat broader posteriorly than anteriorly; crown in occlusal view very slightly concave labially, generally anteriorly converging lingually; longitudinal crest secant, nearly straight, relatively low. Apex of paracone about one-fifth distance along crown from anterior point; crest transected by four sets of vertical labial and lingual ridges with production of cuspules at crest; ridges and cuspules decrease in strength posteriorly. Hypocone moderately strong, connected to metacone by strong, high, labial ridge; posterior ridge from metacone ascends towards crown base; posterior ridge from hypocone curves labially; well defined posterior fossette developed posterior to ridge connecting posterior cusps; anterior ridge from hypocone ascends rapidly to above crown base, then continues anteriorly as low lingual cingulum; ridge from cingulum to paracone not always developed and cingulum continues anteriorly to point slightly linguad to anterior margin of crown; lingual basin shallow, crossed by extensions of ridges from cuspules at crest; cingulum very irregularly sinuous in lingual view; posterior of lingual basin occasionally with well defined tubercle. Base of crown tumid.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in occlusal view; very slightly constricted across median valley; lophs low, slightly bowed anteriorly; metaloph broader than protoloph in M^1 and M^2 , approximately equal in M^3 and somewhat narrower in M^4 . Anterior cingulum low, broad, short, nearly planar transversely; generally no trace of distinct forelink present, but low, weak ridge occasionally passes from base of protoloph to cingulum, near crown axis; anteriorly, cingulum flattened or broadly curved; relatively strong ridge ascends from paracone, uniting with labial margin of cingulum, strongly delimiting labial extremity of cingular shelf; slight anterolingual fossette usually present at lingual extremity of anterior cingular shelf. Midlink relatively strong, moderately low, curving only very slightly posterolabially from protocone to unite with slight ridge from near midpoint of metaloph, above median valley; strong ridge ascends posteriorly from paracone, then curves lingually to cross median valley about one-half way between midlink and labial margin; ridge usually unites with very weak ridge ascending anterolingually from metacone; labial moiety of median valley sharply U-shaped; lingual limit of valley occasionally tuberculate, but usually smooth. Strong slightly flared ridge ascends posterolingually from hypocone to above metacone, uniting with lesser ridge ascending from metacone; posterior fossette well defined, shallow, delimited by ridges from posterior cusps slightly labiad to crown axis.

DISCUSSION: *Protemnodon devisi* sp. nov. is the best represented protemnodont in the Chinchilla fauna. The bulk of the material here referred to *P. devisi*, like that of *P. chinchillaensis* described above, was originally referred by De Vis (1895) to *P. anak*. The species is known only from fragmentary mandibular and maxillary remains and, while no associated cranial remains have been recovered, the maxillae are referred on the basis of both size and morphology.

Table 15 presents summaries of mandibular and maxillary measurements for *P. devisi*, while Table 16 indicates measurements for the holotype, F4710. Variation, as expressed by the Coefficient of Variation, is consistent with that in other species of *Protemnodon*. Generally, the sample is reasonably adequate for mandibular remains but is too small for all but general conclusions on the maxillary characters considered. Morphological variation in the premolar teeth is illustrated in Figure 8.

Plane (1972) considers the possibility that this Chinchilla species may represent a local population of *P. otibandus* Plane, described from the Awe fauna in the Middle Pliocene Otibanda Formation, Bulolo, Papua and New Guinea and recorded by Plane (1972) in the marine Lower Pliocene (Kalinan) Jemmy's Point Formation, Victoria. At present, however, sufficient morphological distinctions are present in the Chinchilla sample, here referred to *P. devisi*, to justify its description as a distinct species, and the Jemmy's Point specimen could equally well relate to this material.

In particular, *P. devisi* is distinguished from *P. otibandus* by its smaller permanent premolars and generally larger molars. The trigonid basin in lower molars is broader in *P. devisi* while the anterior cingulum in upper molars also appears broader. The upper molars are less ovate in occlusal view, and usually have a moderately well defined lingual swelling at the margin of the median valley. The distinct cuspid at the labial end of the talonid basin in M_1 , regarded by Plane (1967) as diagnostic in *P. otibandus*, is not developed in any specimen of *P. devisi*. While no attempt has been made to define post-cranial elements in *P. devisi*, adequate material referable to the genus exists in the Chinchilla Sand collections to ensure representation of both this species and *P. chinchillaensis*. Sufficient differences exist in this material, particularly in the bones of the feet, to suggest that the distinctions outlined for cranial remains are apparently reflected in other skeletal elements.

Compared with *P. chinchillaensis*, *P. devisi* is larger in many of its molar dimensions but it has smaller premolars. Morphologically, *P. devisi* has a more robust ramus, a more elevated symphysis, and lacks the swollen bases to the protolophids so evident in *P. chinchillaensis*. As with all Pliocene species yet described, *P. devisi* has lower crowned teeth than Pleistocene species.

It is evident by comparison with the summary of measurements presented for *P. brehus* (Table 6) that overlap occurs. However, apart from the lower crown heights in *P. devisi*, the species are chiefly distinguished by the generally shallower ramus in the Pliocene form, the lower, less curved links in upper and lower molars and the more labial positioning of these in the lower molars. Compared with *P. roechus*, overlap occurs in many of the characters assessed statistically. Morphologically, the species are separated by many features including the greater elevation of the symphysis and shallower depth of the ramus in *P. devisi*, its lower crowned teeth, its more complex premolar

accessory ridge structure, and the well developed posterior cingulum present in its lower molars. *P. anak* is somewhat smaller than *P. devisi* but again overlap occurs in dental dimensions considered. The species are separated by use of a number of characters including the more elevated nature of the symphysis in *P. devisi*, the lower crown heights present in the Pliocene species, the broader anterior cingulum in its lower molars and the strong accessory ridging in its upper molars.

In addition to the material referred to *P. devisi* from the Chinchilla Sand, the only other specimen from a locality other than this is AM F15464, a left mandibular ramus with M_2 – M_4 , from a well at 125 feet depth, six miles from Mullaley near Coonabarabran, New South Wales. Measurements for this specimen are presented in Table 16.

DISCUSSION

At present, five species of *Protemnodon* Owen are known from the Upper Cainozoic deposits of Queensland, these comprising *P. anak*, *P. brehus*, *P. roechus* from the Pleistocene fluviatile deposits and *P. chinchillaensis* and *P. devisi* from the Late Pliocene Chinchilla Sand. A sixth species, *P. otibandus*, has been recorded from the Lower Pliocene of Victoria. It would appear that the Pleistocene species were widespread throughout Australia, but in many instances critical evaluation of collections made from sites other than in the east coast area will be required before distribution of the species can be more conclusively defined. Of the Pliocene species, *P. chinchillaensis* is restricted to the Chinchilla Sand but *P. devisi* is also recorded from near Mullaley, New South Wales. The specimen referred by Plane (1972) to *P. otibandus* could also relate to this species.

Figure 9 illustrates data derived from the Queensland samples of *Protemnodon* in the form of a log difference diagram (Simpson, 1941). This shows comparatively the proportional relationships of some dental parameters, based on *P. anak* as a standard. It is apparent that *P. brehus* and *P. roechus* are very similar to one another but differ considerably from *P. anak*. In particular the teeth in the larger Pleistocene species are relatively broader than corresponding teeth in *P. anak*. The Chinchilla Sand species have teeth which compare closer in relative proportions with *P. brehus* and *P. roechus* than with *P. anak*. Exceptions to this lie mainly in the permanent premolars in *P. chinchillaensis* which are relatively more elongate than in any other species represented and in the lower heights of the molar teeth in the Late Pliocene species. This latter feature is consistently observed in all known Pliocene species and increase in height of crown would appear to represent one of the Upper Cainozoic evolutionary trends.

The origins of *Protemnodon* are obscure although Stirton *et al.* (1967b) record the presence of a protemnodont in the Late Oligocene or Early Miocene Wipijiri Formation, Tirari Desert, while Woodburne (1967) records a possible protemnodont in the Late Miocene or Early Pliocene Alcoota fauna from the Waite Formation in central Australia. The species *Hadronomas puckridgei* Woodburne, also described from the Alcoota fauna and suggested by Woodburne (1967) as being close to the lineage leading to the Sthenurinae, could equally well be considered near the lineage leading to the Upper Cainozoic protemnodonts (Bartholomai, 1972a). Within the group it appears likely that

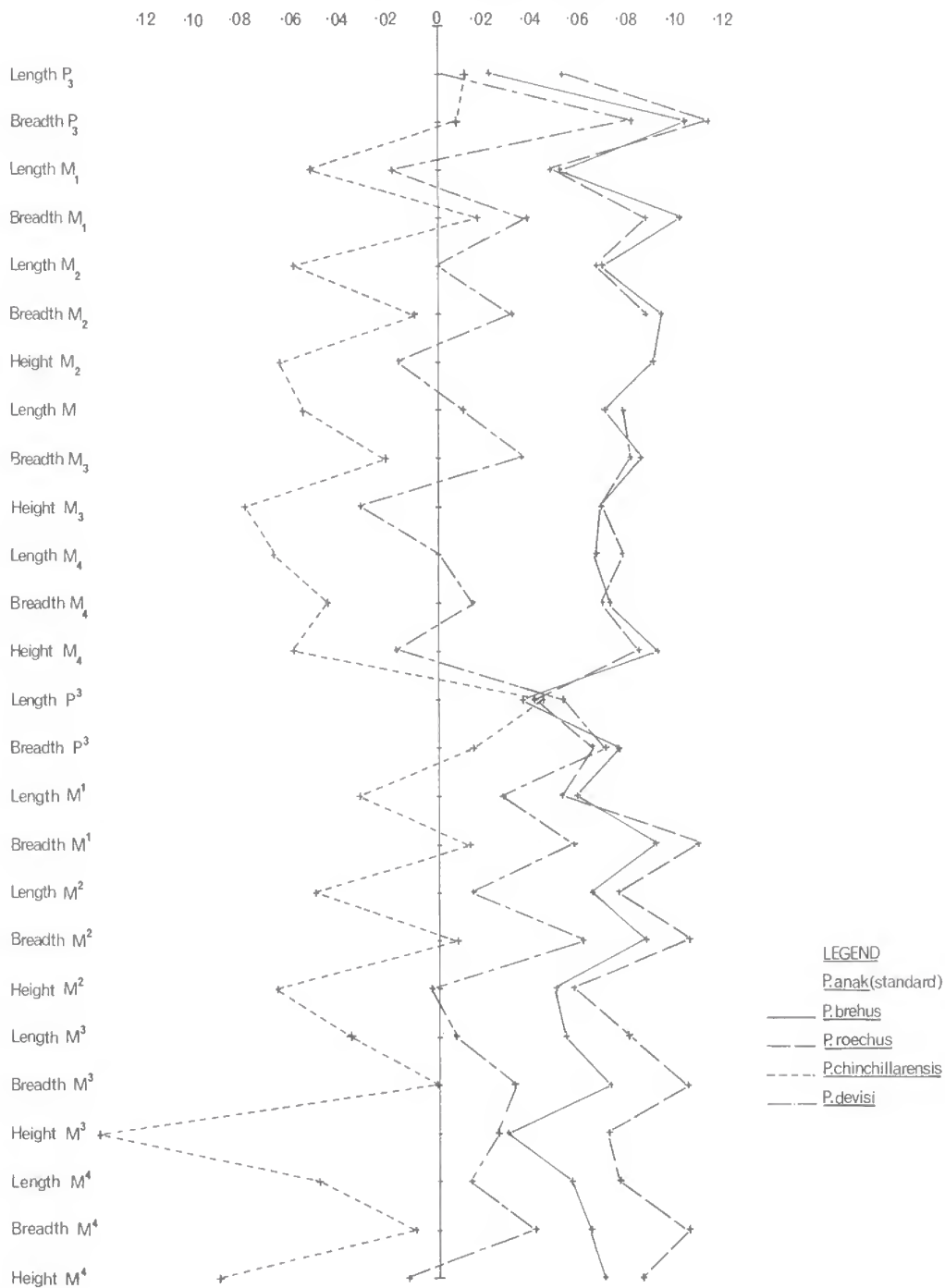


FIG. 9: Log Difference Diagram indicating the proportional relationships of mean values of samples of lower and upper permanent cheek teeth in *Protomnodon* spp., utilizing data for the mean of *P. anak* as standard. Mean values for each species have been connected to facilitate comparison.

P. devisi is closely related to *P. otibandus* on the one hand and to *P. brehus* and *P. roechus* on the other. *P. chinchillaensis* may relate with *P. anak* in the Pleistocene but morphological support for this is not as strong as for the relationships of *P. devisi*.

It is obvious from what is known of the morphology of *Protemnodon* that the genus was adapted primarily as a grazing animal and its relative abundance in the Pleistocene fluvial deposits of the Darling Downs area is in keeping with the proposals that the region during that time comprised well watered, open sclerophyll and open grassland areas ideally suited to grazing and browsing macropodids. Similar palaeoecological conditions are proposed for the Late Pliocene situation in the western Darling Downs area.

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PLATE 9

Protemnodon anak Owen, 1874

FIG. 1: Lateral view of incomplete cranium, F616, eastern Darling
Downs, $\times \frac{1}{2}$.

FIG. 2: Occlusal view of F616, $\times \frac{1}{2}$.

FIG. 3: Lateral view of partial right premaxilla, F3672, showing
vestigial C¹, Ravensthorpe, Pilton, Darling Downs, $\times 1$.

FIG. 4: Lateral view of partial premaxillae, F651, Gowrie, eastern Darling Downs, $\times 1$.

FIG. 5: Occlusal view of F651, $\times 1$.

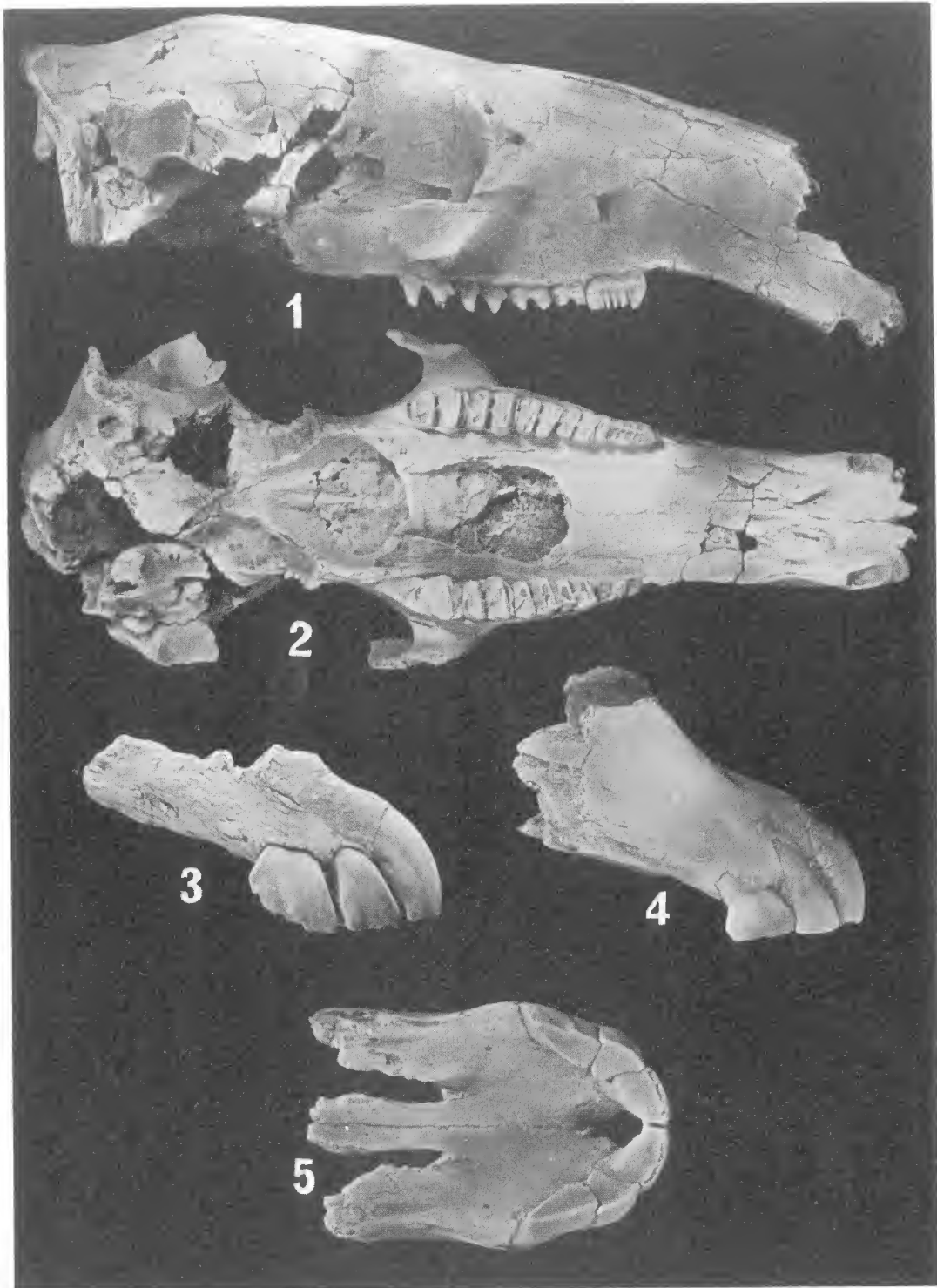


PLATE 10

Protemnodon anak Owen, 1874

- FIG. 1: Lateral view of incomplete juvenile maxilla, F3677, eastern Darling Downs, $\times 1$.
FIG. 2: Stereopair of occlusal view of F3677, $\times 1$.
FIG. 3: Lateral view of incomplete adult maxilla, F4896, Gowrie, Darling Downs, $\times 1$.
FIG. 4: Stereopair of occlusal view of F4896, $\times 1$.

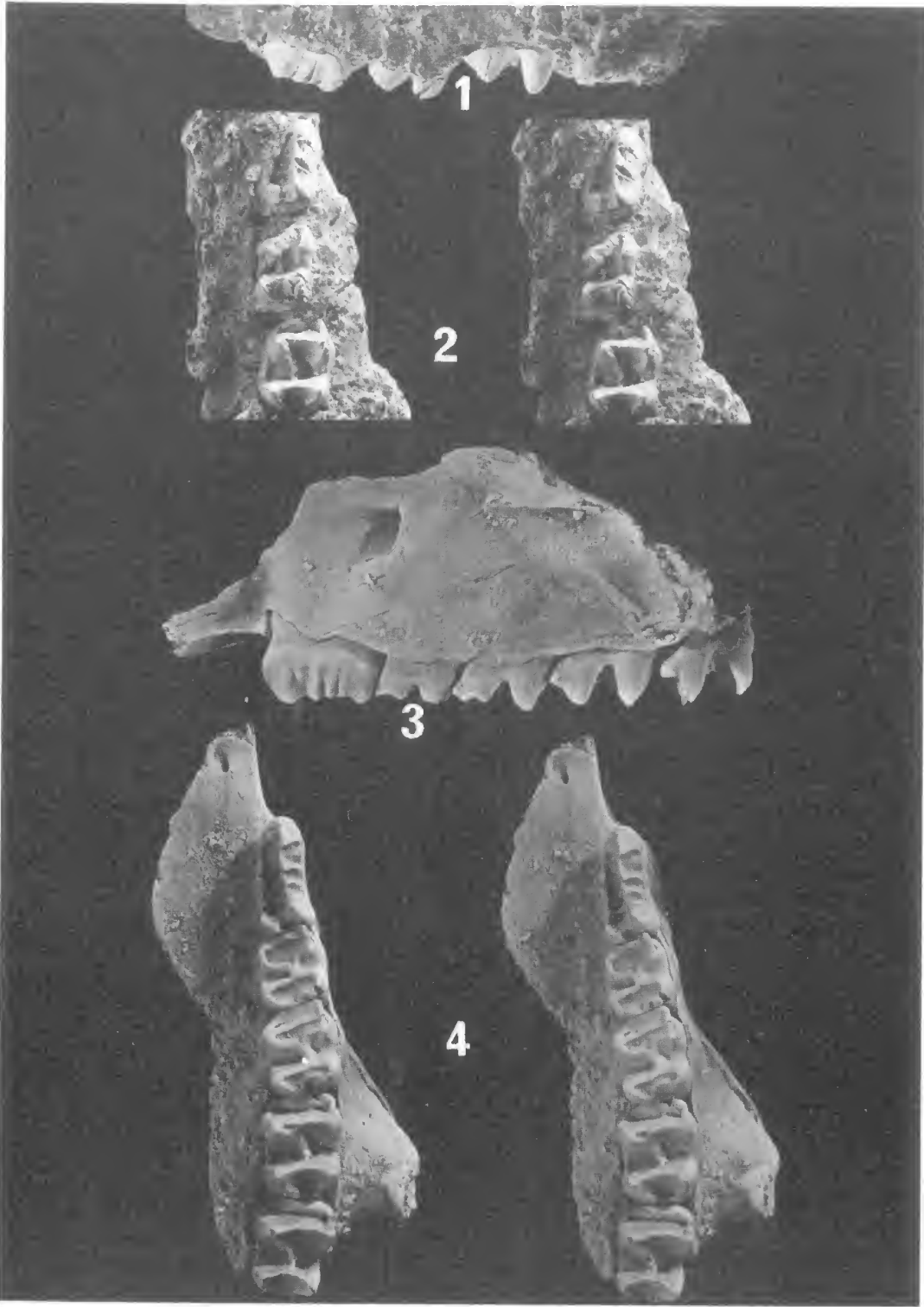


PLATE 11

Protemnodon anak Owen, 1874

FIG. 1: Stereopair of occlusal view of juvenile mandibular rami, F3051,
Gowrie, Darling Downs, $\times 1$.

FIG. 2: Lateral view of F3051, $\times 1$.

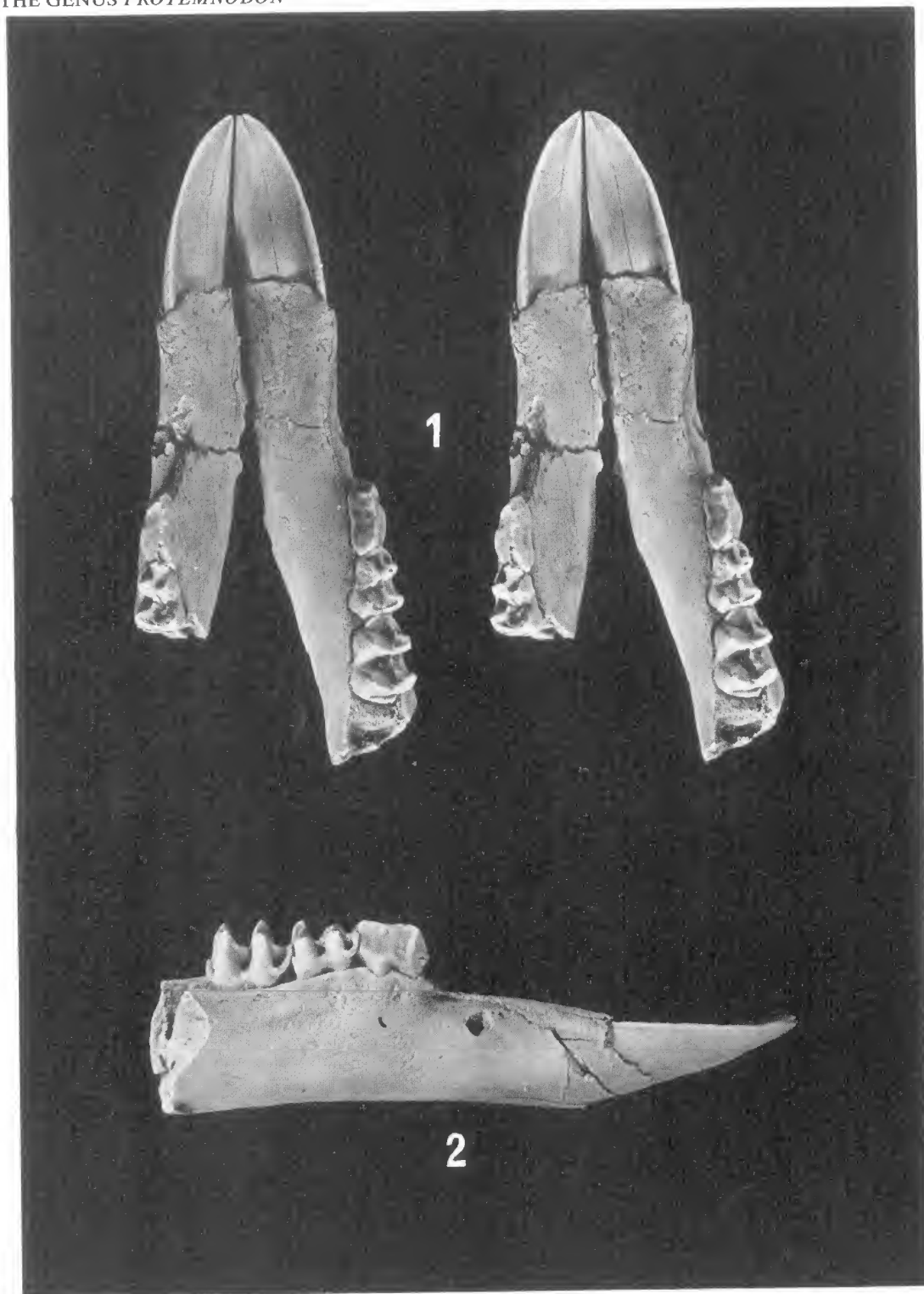


PLATE 12

Protemnodon anak Owen, 1874

FIG. 1: Lateral view of adult mandible, F3034, eastern Darling Downs.
× 1.

FIG. 2: Stereopair of occlusal view of F3034, × 1.

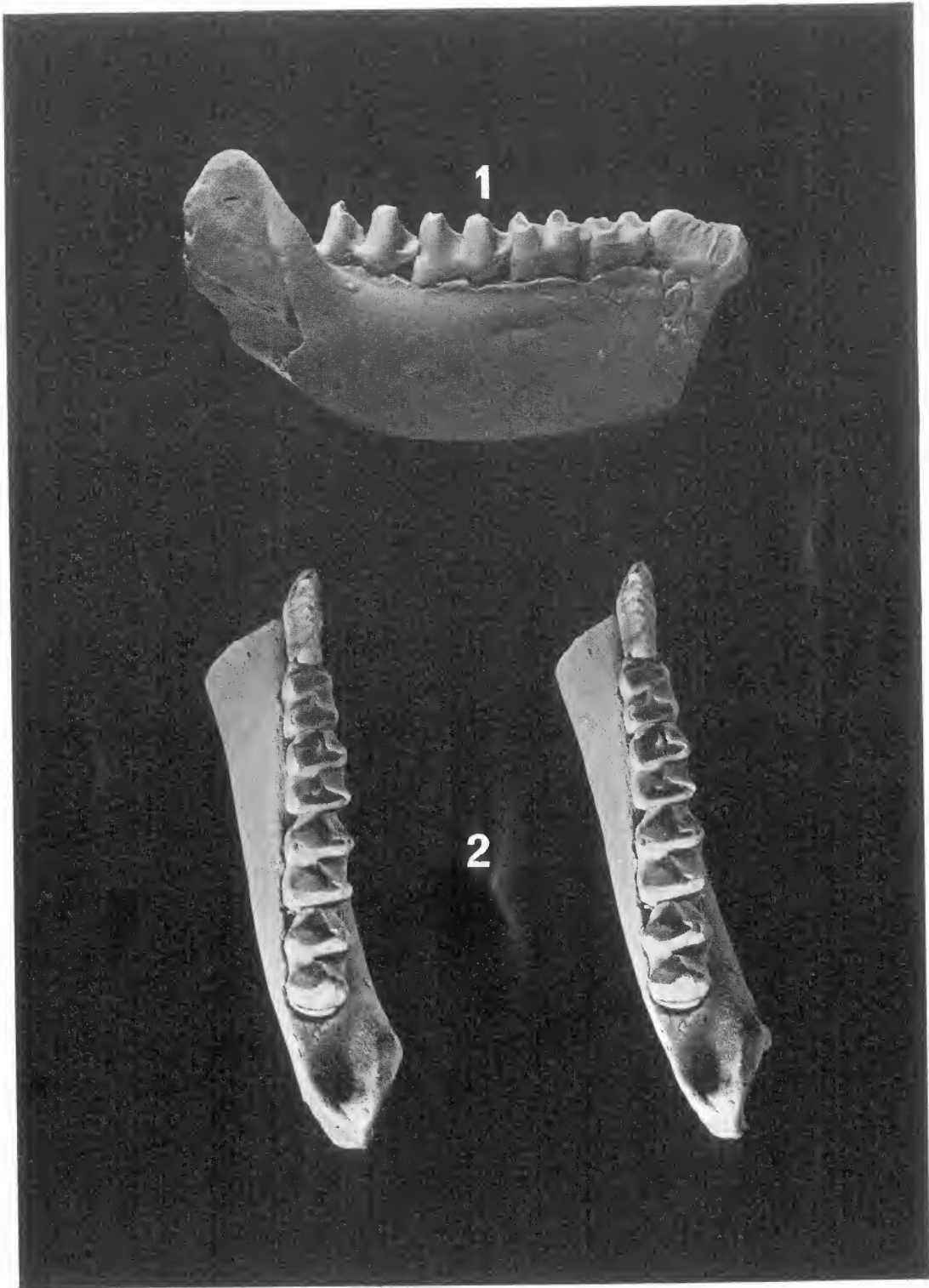


PLATE 13

Protemnodon brehus (Owen, 1874)

FIG. 1: Lateral view of adult maxilla, F4947, eastern Darling Downs,
× 1.

FIG. 2: Stereopair of occlusal view of F4947, × 1.

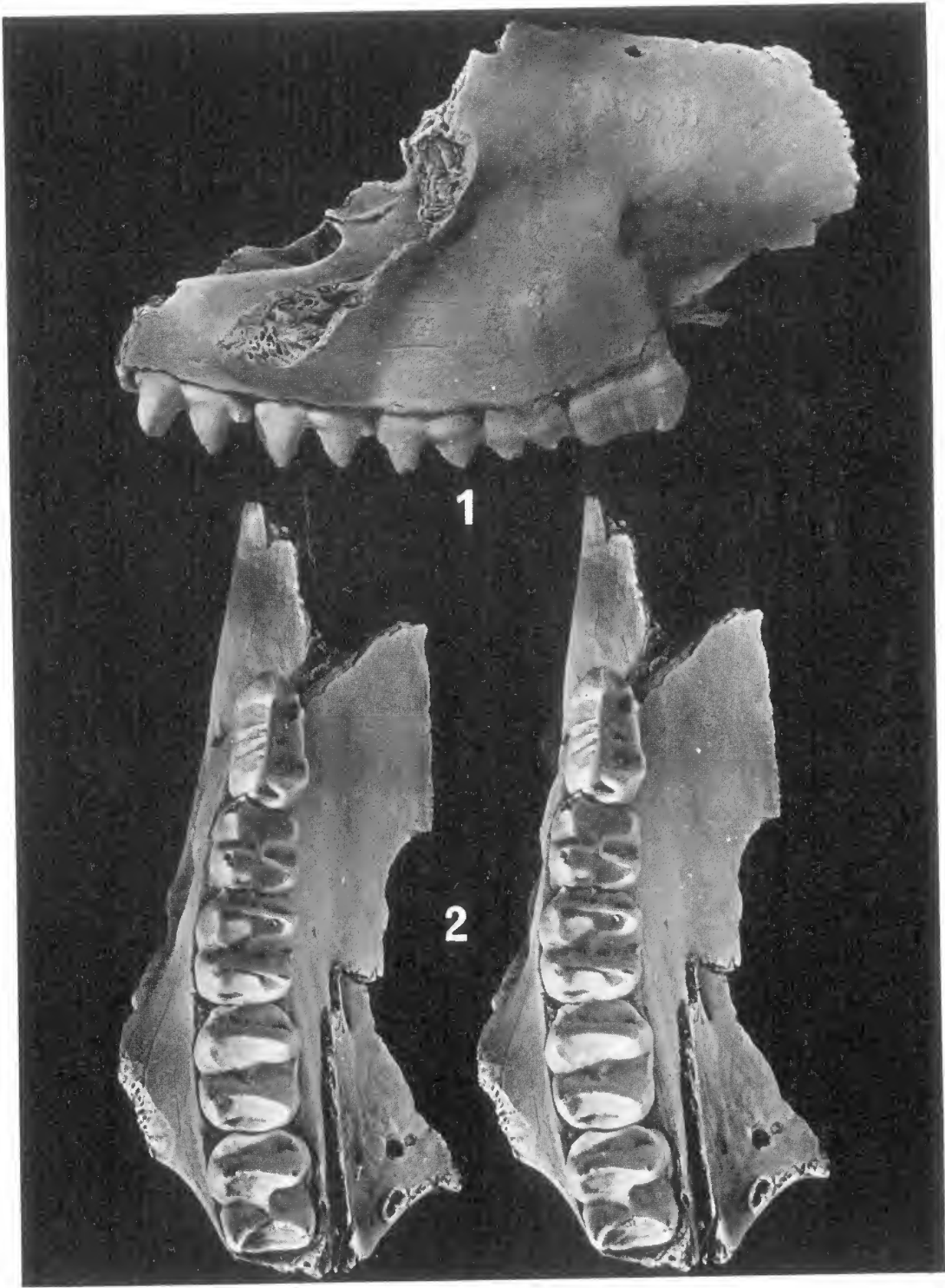


PLATE 14

Protemnodon brehus (Owen, 1874)

FIG. 1: Lateral view of juvenile mandible, F3027, eastern Darling
Downs, $\times 1$.

FIG. 2: Stereopair of occlusal view of F3027, $\times 1$.

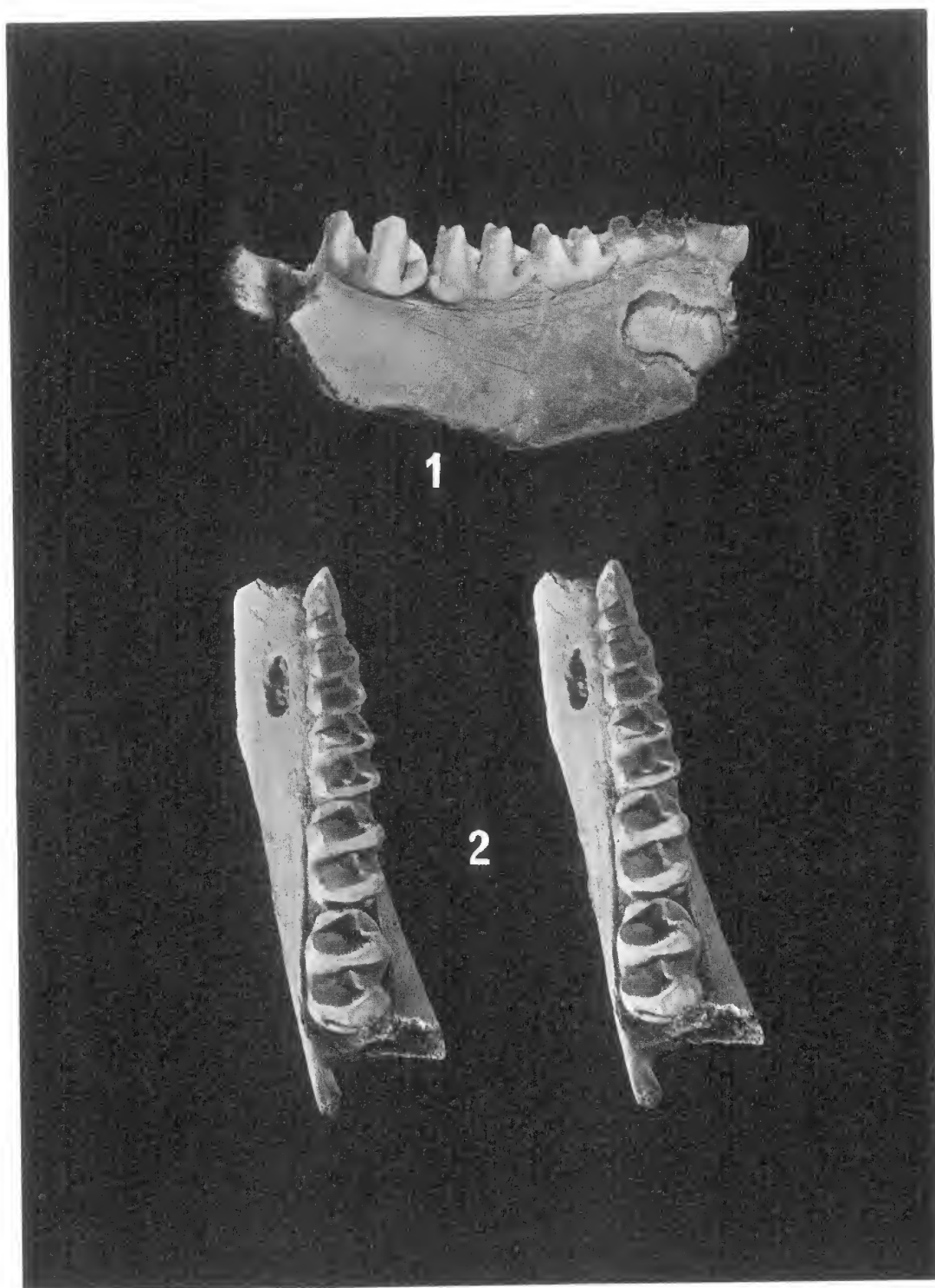


PLATE 15

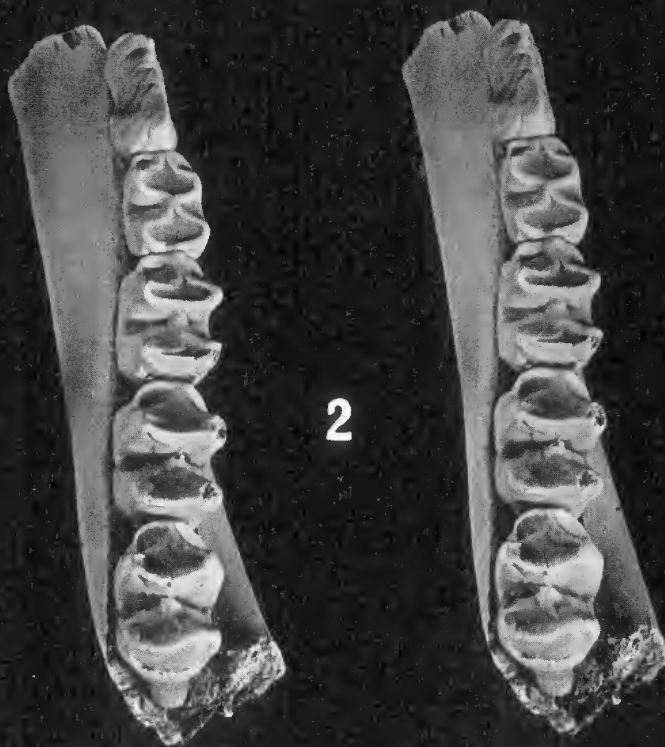
Protemnodon brehus (Owen, 1874)

FIG. 1: Lateral view of adult mandible, F3029, eastern Darling Downs,
× 1.

FIG. 2: Stereopair of occlusal view of F3029, × 1.



1



2

PLATE 16

Protemnodon roechus Owen, 1874

FIG. 1: Labial view of partial premaxilla, F5053, eastern Darling Downs, $\times 1$.

FIG. 2: Stereopair of occlusal view of F5053, $\times 1$.

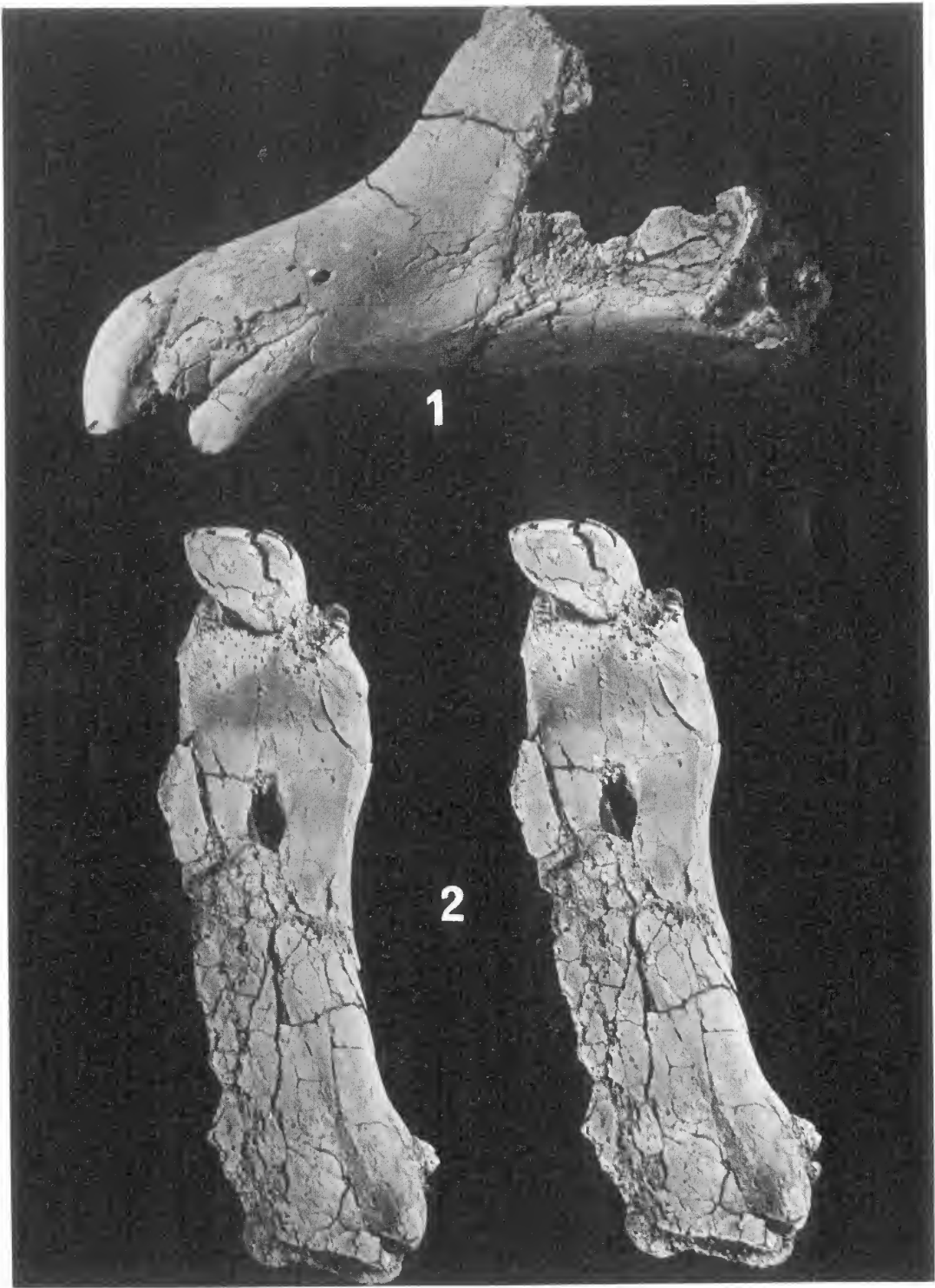


PLATE 17

Protemnodon roechus Owen, 1874

FIG. 1: Labial view of adult maxilla, F4948, eastern Darling Downs,
× 1.

FIG. 2: Stereopair of occlusal view of F4948, × 1.

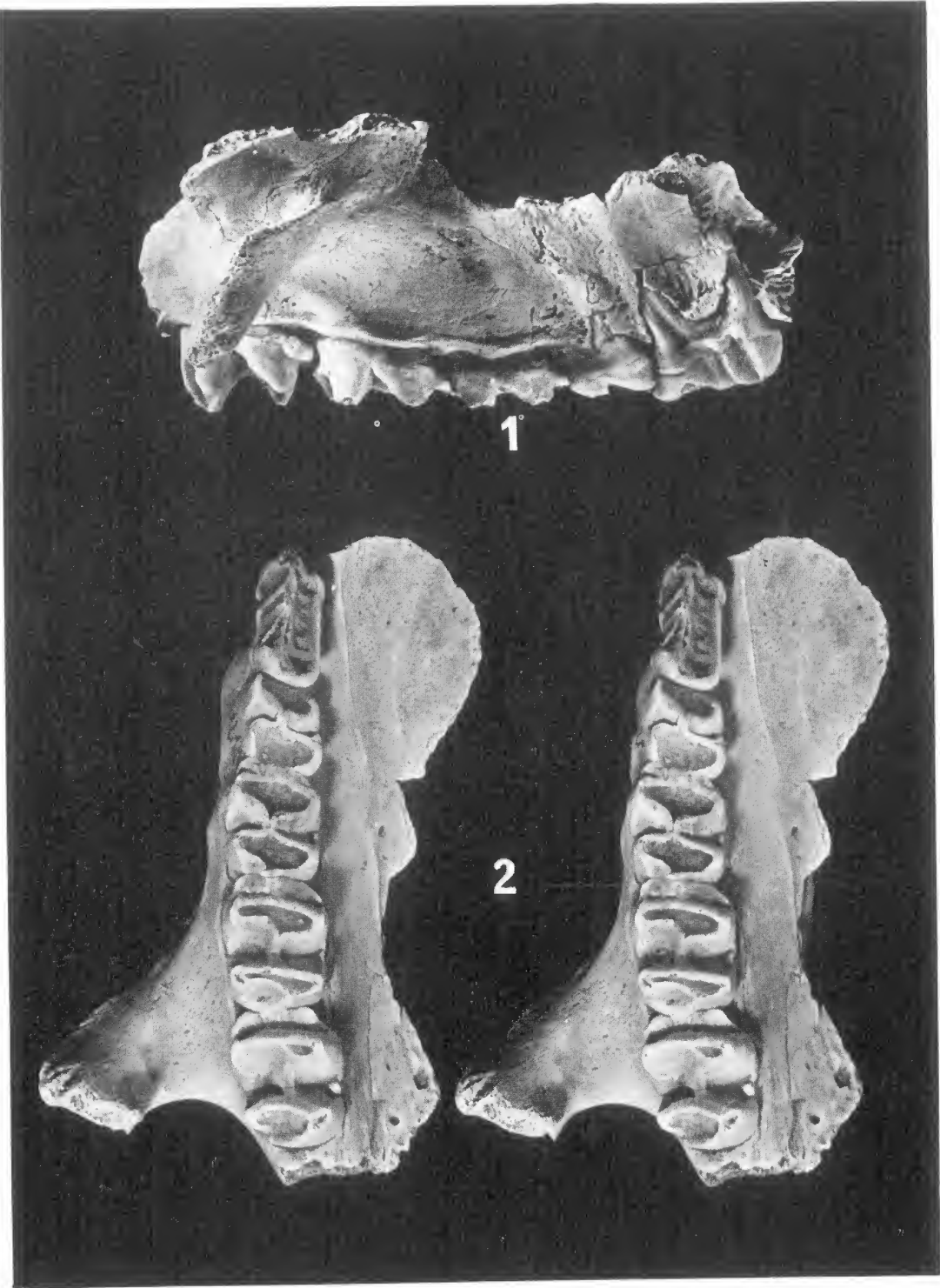


PLATE 18

Protemnodon roechus Owen, 1874

FIGS. 1, 1a: Occlusal view of partial associated juvenile mandibular rami with stereopair of right mandible, F647, eastern Darling Downs, $\times 1$.

FIG. 2: Lateral view of F647, $\times 1$.

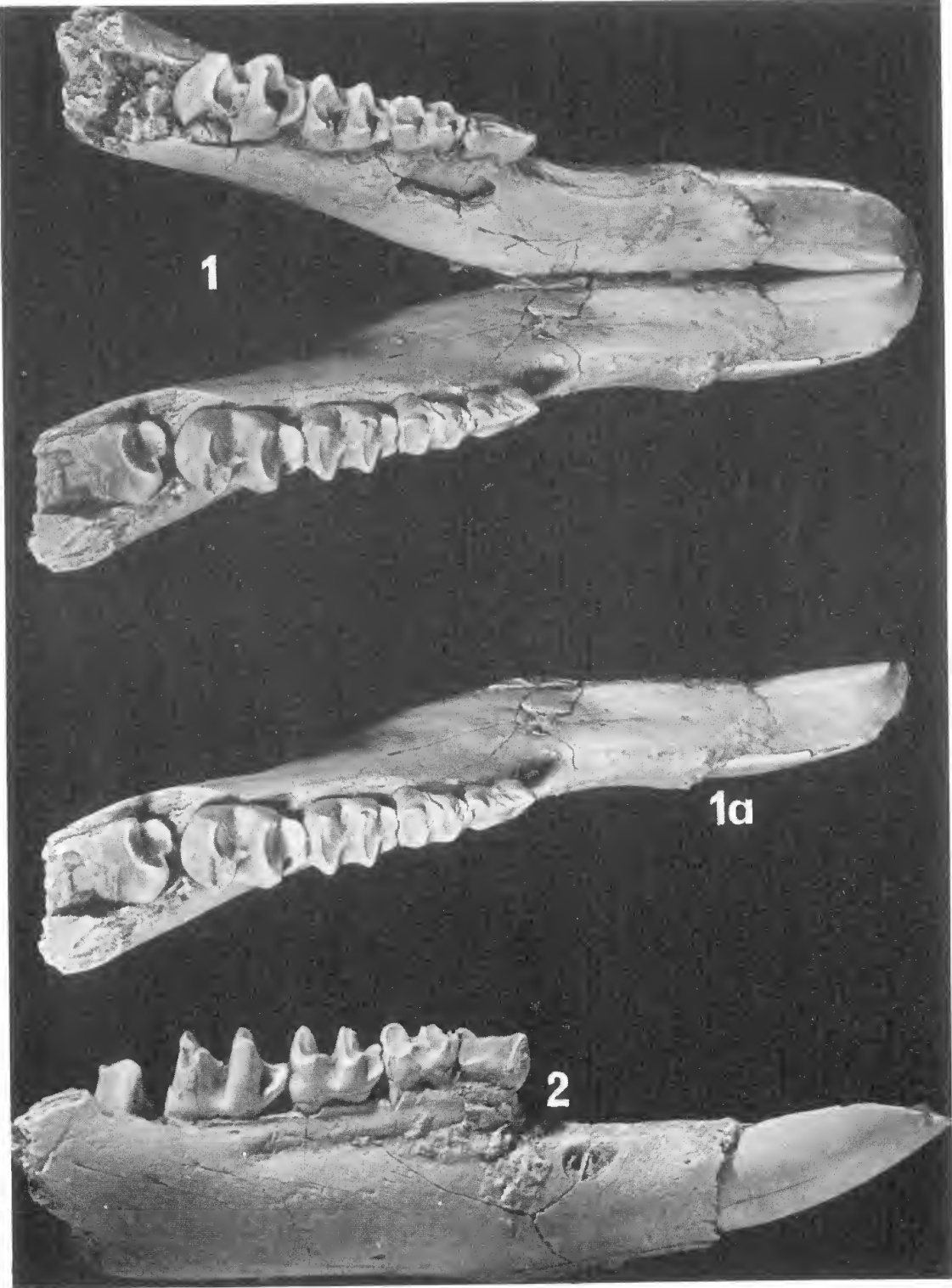


PLATE 19

Protemnodon roechus Owen, 1874

FIG. 1: Labial view of partial adult mandible, F3033, eastern Darling
Downs, $\times 1$.

FIG. 2: Stereopair of occlusal view of F3033, $\times 1$.

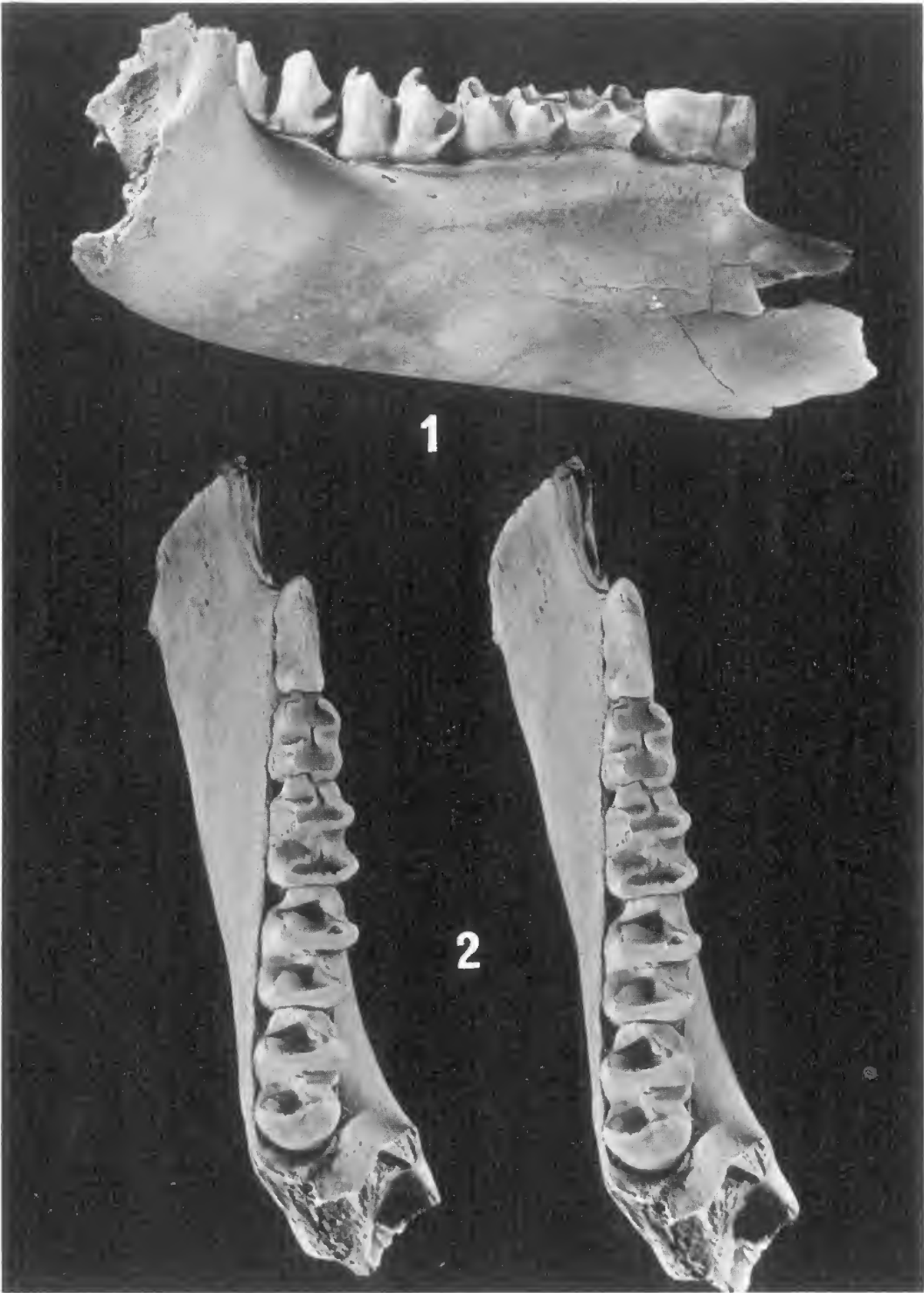


PLATE 20

Protemnodon chinchillaensis sp. nov.

- FIG. 1: Lateral view of partial juvenile maxilla, F5239, western Darling Downs, $\times 1$.
FIG. 2: Stereopair of occlusal view of F5239, $\times 1$.
FIG. 3: Lateral view of partial adult maxilla, F4719, Chinchilla, Darling Downs, $\times 1$.
FIG. 4: Stereopair of occlusal view of F4719, $\times 1$.

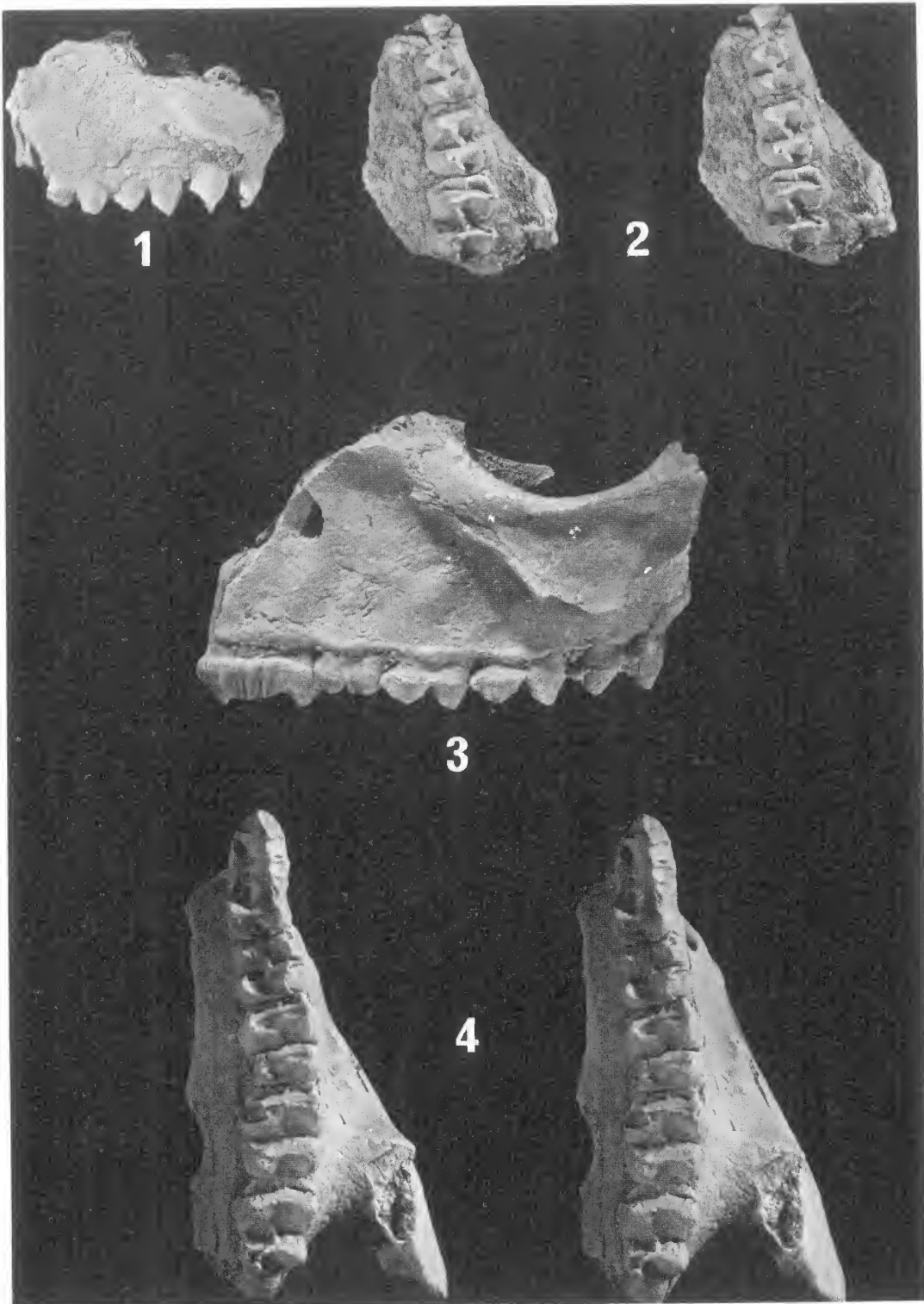


PLATE 21

Protemnodon chinchillaensis sp. nov.

- FIG. 1: Lateral view of partial juvenile mandible, F5242, Chinchilla, Darling Downs, $\times 1$.
FIG. 2: Stereopair of occlusal view of F5242, $\times 1$.
FIG. 3: Lateral view of holotype, partial adult mandible, F5246, Chinchilla, Darling Downs, $\times 1$.
FIG. 4: Stereopair of occlusal view of holotype, F5246, $\times 1$.

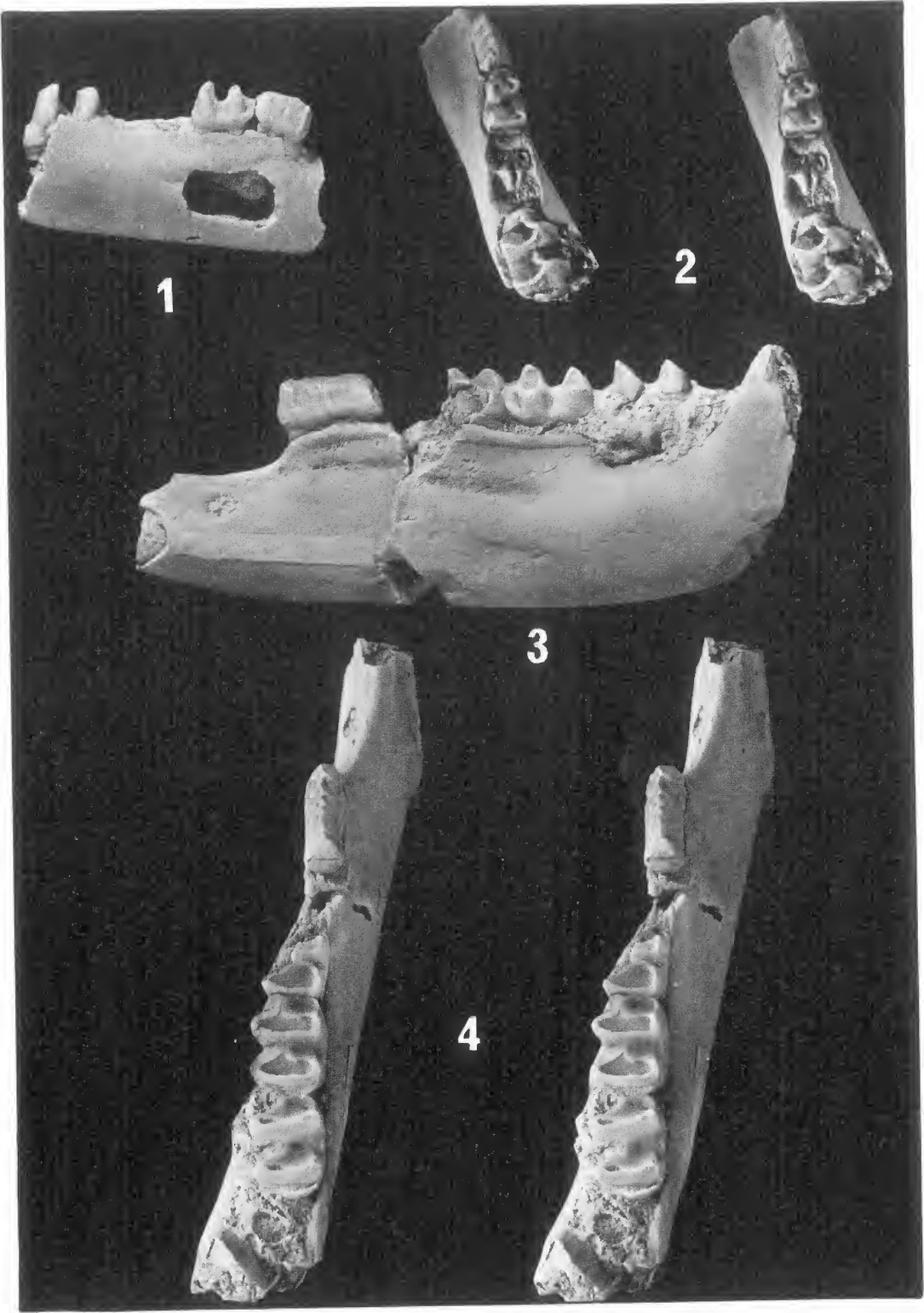


PLATE 22

Protemnodon devisi sp. nov.

FIG. 1: Lateral view of partial adult maxilla, F4688, western Darling Downs, $\times 1$.

FIG. 2: Stereopair of occlusal view of F4688, $\times 1$.

FIG. 3: Lateral view of partial juvenile maxilla, F4712, Chinchilla, Darling Downs, $\times 1$.

FIG. 4: Stereopair of occlusal view of F4712, $\times 1$.

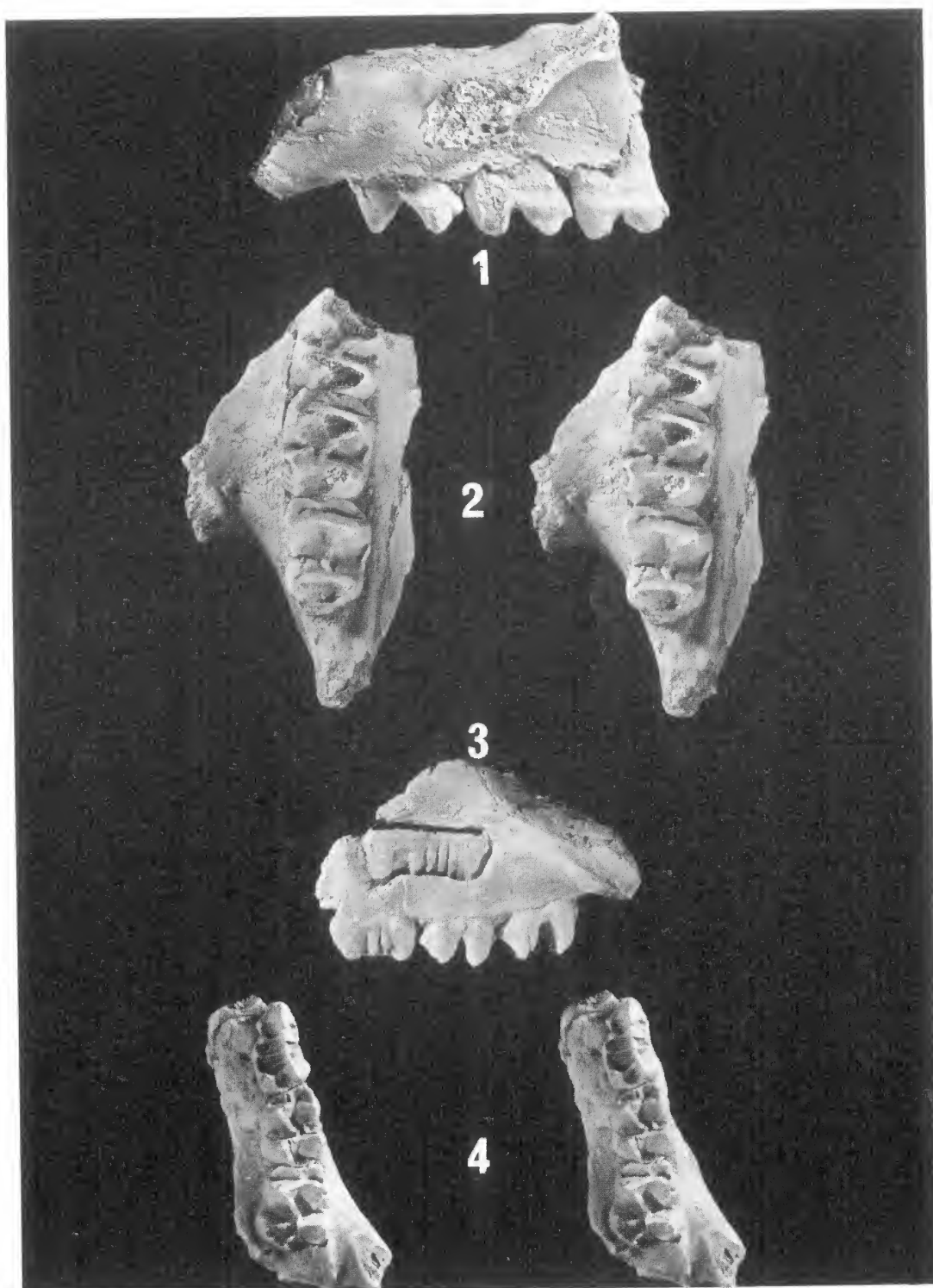


PLATE 23

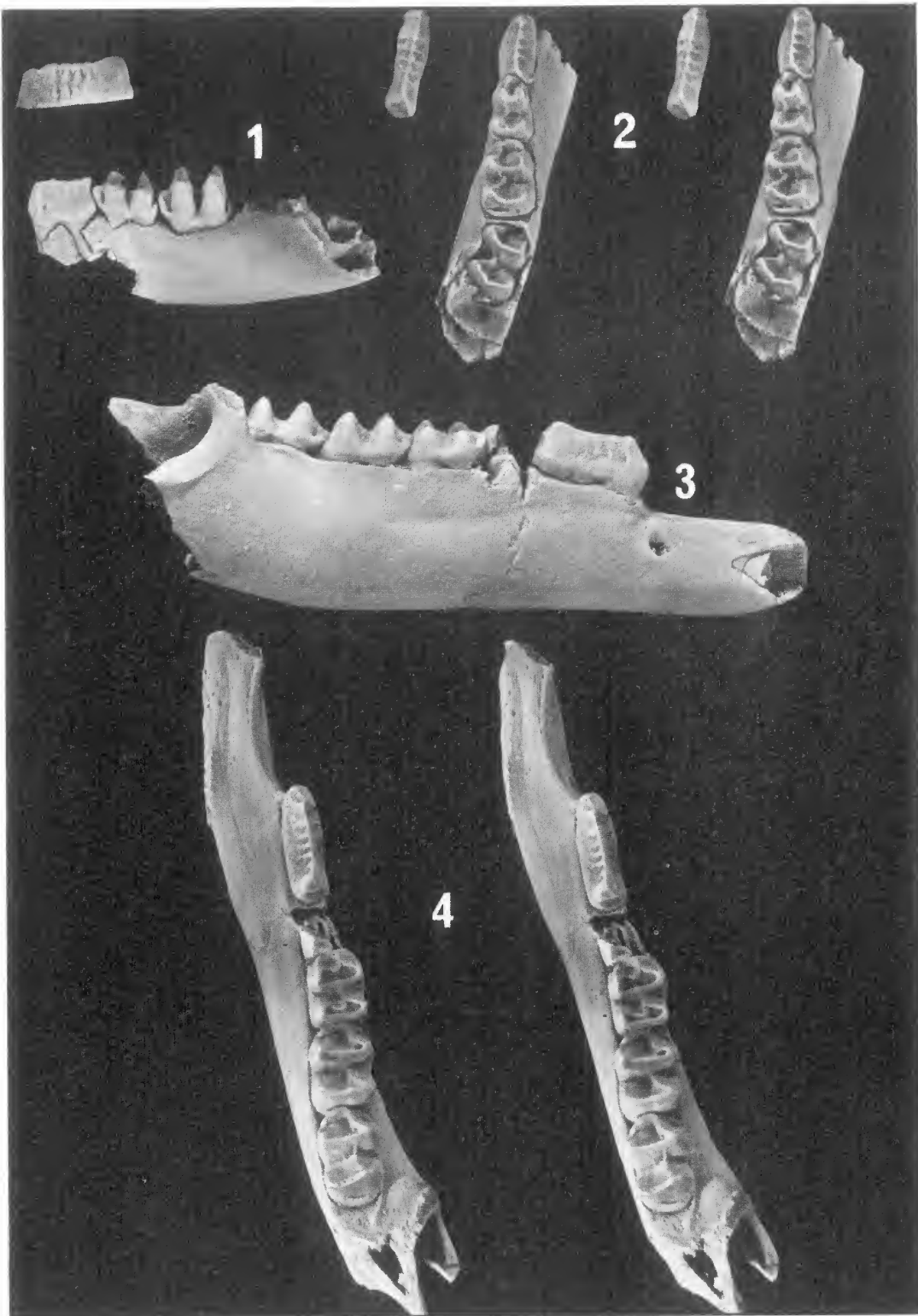
Protemnodon devisi sp. nov.

FIG. 1: Lateral view of partial juvenile mandible with excavated P_3 , F4797, western Darling Downs, $\times 1$.

FIG. 2: Stereopair of occlusal view of F4797, $\times 1$.

FIG. 3: Lateral view of holotype, partial adult mandible, F4710, Chinchilla, Darling Downs, $\times 1$.

FIG. 4: Stereopair of occlusal view of holotype, F4710, $\times 1$.





FISSURIDON PEARSONI, A NEW FOSSIL MACROPODID
(MARSUPIALIA) FROM QUEENSLAND

ALAN BARTHOLOMAI
Queensland Museum

ABSTRACT

A new fossil macropodid, *Fissuridon pearsoni*, is described from the Pleistocene fluviatile deposits of the eastern Darling Downs area, southeastern Queensland. The species is at present known only from fragmentary mandibular specimens and comprises one of the rarest forms yet recorded from the diverse fauna of those sediments.

The fauna from the Pleistocene fluviatile deposits of the eastern Darling Downs area, southeastern Queensland included a diverse assemblage of browsing and grazing macropodids, many of which were widespread throughout mainland Australia at that time. Bartholomai (1963, 1966, 1967, 1970, 1972) has previously investigated aspects of the fossil Macropodidae of Queensland and the present contribution represents a continuation of that part of the faunal study.

The material comprising the present sample was, in part, considered by De Vis (1895) but its distinctness was not formally recognized. None of the specimens was illustrated nor specifically mentioned by De Vis (1895) so doubt exists regarding the taxon under which they were included at that time. Four of the paratypes bear the manuscript name '*Macropus pales*' in De Vis's handwriting. The specimen selected as holotype was donated to the Queensland Museum by the late Mr W. H. Pearson of Clifton, whose collections have done so much to improve knowledge of the Pleistocene fossil marsupials of the Darling Downs area. The species is named after him.

All measurements throughout are in millimetres.

Genus *Fissuridon* nov.

TYPE SPECIES: *Fissuridon pearsoni* sp. nov.

DIAGNOSIS: The characters of this genus are those of the type species until any other species is described.

***Fissuridon pearsoni* sp. nov.**

(Pl. 24, figs. 1-4; pl. 25, figs. 1-2)

MATERIAL: Holotype, F3921, partial left mandibular ramus with M_1 - M_2 , P_3 exposed by fenestration, and M_3 unerupted but loose in the ramus, juvenile, King Creek, near M.R. 039454 Clifton 1 mile map, southeastern Queensland, from Pleistocene fluvial deposits.

F1656, partial left mandibular ramus with M_4 broken, adult, Dalby, Darling Downs, F3922, partial left M_4 , adult, 'Sharrow' (Harrow, Cambooya), Darling Downs, F3925, partial right mandibular ramus with M_3 , M_4 unerupted, juvenile, Darling Downs. F3926, partial right M_4 , adult, Darling Downs. F3927, partial right mandibular ramus with M_4 , adult, Darling Downs. F3928, isolated right M_4 , Darling Downs. F3930, partial right mandibular ramus with I_1 incomplete, M_1 - M_3 , juvenile, near Dalby, ?Condamine River at Springvale, Darling Downs. F5440, partial right mandibular ramus with partial M_3 , M_4 , adult, Condamine River, at M.R. 058407 Dalby 1 mile map, Darling Downs.

SPECIFIC DIAGNOSIS: Species moderately large. P_3 small, with bifid longitudinal crest. Molars with extremely high, slightly anteriorly rotated lophs, with anterior cingulum high, raised to slightly more than three-quarters the height of protolophid; links high; extremely deep groove descends posterior surface hypolophid, from near hypoconid to point mesiad to posterolingual base of crown, flanked by slightly flared, strong ridge from hypoconid to posterolingual crown base; hypoconid rotated anterolingually to above axis of crown, with associated reduction in width of unworn hypolophid; protoconid also slightly rotated anterolingually.

DESCRIPTION: Mandible relatively deep, strong, but comparatively narrow below anterior cheek teeth, with longitudinal axis moderately concave laterally.

Symphysis elongate, not ankylosed, deflected ventrally at low angle to base of ramus; geniohyal pit relatively deep, low, slightly anterior to posterior symphyseal limit. Diastema elongate. Ventral margin of ramus broadly rounded posterior to symphysis. Mental foramen relatively large, close to and about one-half distance along diastema. Ramus with slight labial groove below anterior cheek teeth, immediately below alveolar margin. Lingually, slight depression present dorsal to base of mandible, leading

TABLE 1
MEASUREMENTS FOR *Fissuridon pearsoni* SP. NOV.

Specimen	P_3	M_1	M_2	M_3	M_4
F3921*	7.3 × 3.5	14.3 × 8.4	17.0 × 9.8	19.8 × 10.6	—
F3925	—	—	—	18.8 × 10.2	—
F3927	—	—	—	—	22.9 × 12.3
F3928	—	—	—	—	22.7 × 11.7
F3930	—	—	16.9 × 9.5	19.5 × 10.5	—
F5440	—	—	—	—	20.5 × 10.9

* Holotype *Fissuridon pearsoni* sp. nov.

posteriorly into pterygoid fossa. Post-alveolar shelf short, leading to post-alveolar ridge ascending onto mesial wall of coronoid process, above mandibular foramen. Anterior wall of coronoid process reclining slightly. Angle of mandible, condyle and bulk of coronoid process not preserved.

I₁ elongate, nearly horizontal, lanceolate, curving lingually and approximated ventrally towards tip, with resultant mesial facet of wear. Crown blade-like, with enamel flanged dorsolabially and ventrolingually; enamelled laterally, ventromesially to about one-half depth of tooth from below, and mesially to slightly below dorsolabial flange. Surface of wear with upper incisors subhorizontal, near planar.

P₂ and DP₃ unknown.

P₃ very small, weak, subovate in basal outline, being only very slightly narrower anteriorly than posteriorly, and being extremely slightly constricted mesially. Longitudinal crest bifid, slightly subdivided posterior to mid-point by weak, vertical, labial and lingual grooves; crest continues posterolingually from posterior cuspid towards base of crown. Crown base slightly swollen lingually, anteriorly and labially.

M₁ < M₂ < M₃ < M₄; molars subrectangular, slightly constricted across talonid basin; lophids extremely high, with protolophid slightly convex posteriorly in occlusal view, but with hypolophid exhibiting considerably greater curvature; hypolophid approximately as broad as protolophid in M₁ and M₂, but slightly narrower in M₃ and M₄. Trigonid basin broad, moderately long, its length approximately equalling distance between lophid crests, more restricted labially than lingually, with development of anterolabial fossette. Forelink extremely high, strong, descending only slightly from protoconid to anterior cingulum, slightly labial to mid-point; occasionally ornamented by slight vertical ridges. Anterior cingulum extremely high, being raised slightly more than three-quarters the height of protolophid; in slightly worn teeth, cingulum represents a third major transverse grinding surface. Protoconid somewhat rotated anterolingually, producing slightly anteriorly rotated protolophid; labial base of protolophid considerably larger than lingual, with anterolabial surface below protoconid usually rounded, but occasionally forming well-defined angular ridge to trigonid; labial surface usually with slight, variable, broad, vertical grooves; slight ridges descend anteriorly and posteriorly from metaconid, with posterior ridge occasionally well developed; protolophid crest generally cleft by slight anterior and posterior vertical grooves, about one-half distance between cuspids. Midlink from hypoconid extremely high, strong, descending slightly anterolingually to unite with strong posterolingual ridge from protoconid above talonid basin; ridges usually not abutting exactly, frequently over-riding one another, with junction marked by vertical labial and lingual grooves. Talonid basin slightly constricted, sharply V-shaped in labial moiety, but broadly U-shaped and elevated lingually; lingual moiety basally with variably developed, generally broad, low, transverse ridges. Hypoconid considerably rotated anterolingually, being positioned above axis of crown, with hypolophid exhibiting considerable anterior rotation; labial base of hypolophid considerably larger than lingual, with anterolabial surface below hypoconid usually broadly angled as ridge to talonid; labial surface usually with variable, broad, vertical grooves; extremely slight, variable ridges descend anteriorly and posteriorly from entoconid, with anterior ridge occasionally well developed; hypolophid crest narrow, generally

cleft by vertical anterior and posterior grooves. Posterior surface of hypolophid with deep, gaping groove, descending diagonally from near hypoconid to point mesiad to posterolingual base of crown; strong ridge from hypoconid descending to posterolingual base of crown flanking groove; ridge slightly flared, separated from posterior surface of crown by slight parallel groove. Posterolingual fossette occasionally present at base of groove.

DISCUSSION: Remains of *Fissuridon pearsoni* sp. nov. are not abundant in the Pleistocene deposits of Queensland, but because of the structure of the lower molar teeth the species is readily separable from other contemporary fossil macropodines and also from modern species. The characteristic gaping, diagonal groove on the posterior surface of the hypolophid and the extremely high, lophid-like anterior cingulum are quite distinct in unworn teeth, and are emphasized with wear. The upper dentition is not known as yet, although a single maxilla, F1787, exhibiting molars with high lophids and strong links may be referable to the species.

Compared with other Upper Cainozoic species, the molars in *F. pearsoni* show some resemblance to those in *Macropus titan* Owen, *M. ferragus* (Owen) and *M. pan* De Vis. However, the intraspecific morphological differences between the teeth within the species is considerably less than that between any of them and *F. pearsoni*. In *M. titan*, the posterior surface of the hypolophid is generally marked by a moderately slight, broad groove, terminating basally in a sharply defined, flared, posterolingual fossette, while in *M. ferragus* a shallow to moderate, near vertical groove descends linguad to the axis of the crown. *M. pan* frequently possesses a better defined, more oblique groove than *M. ferragus* but this in no way approaches the extreme development present in *F. pearsoni*.

The species is one of the largest fossil species of *Macropus* yet recorded and a table of measurements for the referred sample is provided in Table 1. The sample is too small to enable any meaningful statistical evaluation to be undertaken.

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PLATE 24

Fissuridon pearsoni sp. nov.

FIG. 1: Lateral view of holotype, F3921, King Creek, near M.R. 039454 Clifton 1 mile map, SE.Q., $\times 1$.

FIG. 2: Stereopair of occlusal view of F3921, $\times 1$.

FIG. 3: Lateral view of F3927, Darling Downs, SE.Q., $\times 1$.

FIG. 4: Stereopair of occlusal view of F3927, $\times 1$.

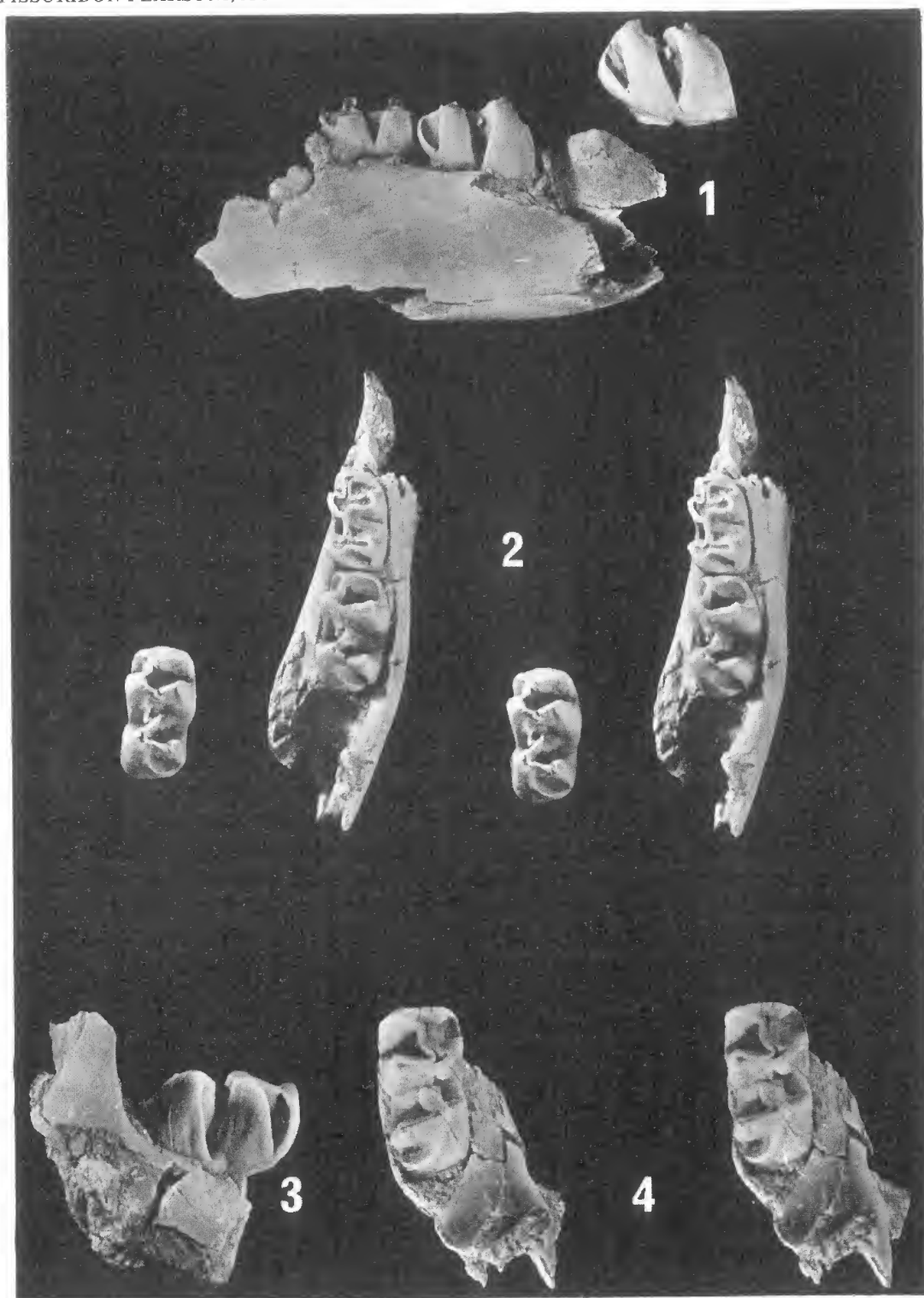
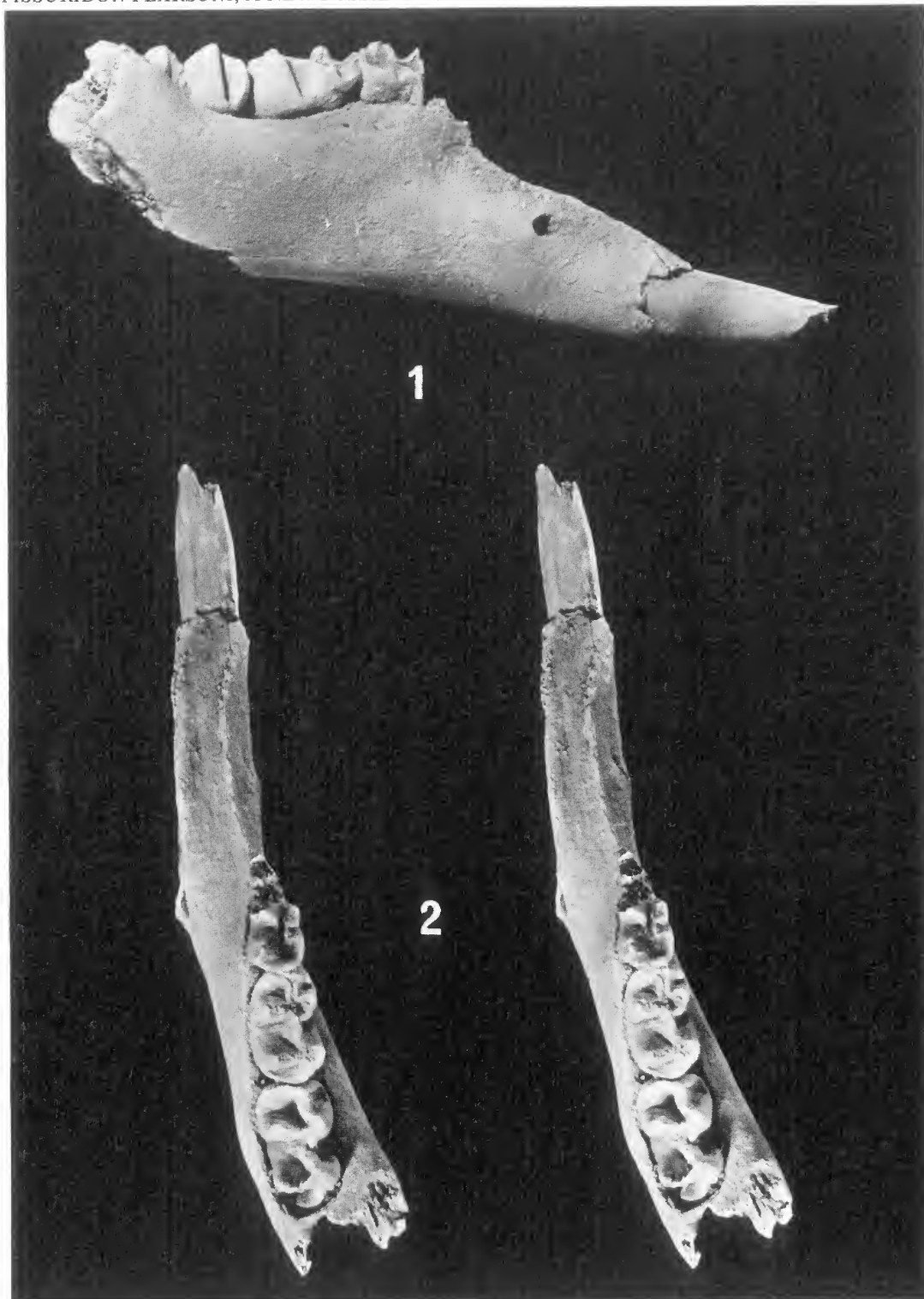


PLATE 25

Fissuridon pearsoni sp. nov.

FIG. 1: Lateral view of F3930, near Dalby, ? Condamine River at Springvale, SE.Q., $\times 1$.

FIG. 2: Stereopair of occlusal view of F3930, $\times 1$.





THE IDENTITY OF THE SUPPOSED DASYURID MARSUPIAL, *SARCOPHILUS*
PRIOR DE VIS, 1883, WITH COMMENTS ON OTHER REPORTED 'PLIOCENE'
OCCURRENCES OF *SARCOPHILUS*

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ABSTRACT

The holotype of *Sarcophilus prior* De Vis, 1883, is redescribed and the specimen is shown to bear closer relationship with the family Vombatidae and in particular with the genus *Vombatus*, than with the family Dasyuridae. A re-examination of reported 'Pliocene' occurrences of *Sarcophilus* shows that these localities are, in fact, of late Pleistocene or Holocene age and that the referred specimens are assignable to either the late Pleistocene species, *S. lanarius*, or the living species, *S. harrisii*.

Stirton (1957) described a large dasyurid, *Glaucodon ballaratensis*, from a well near Smeaton, Victoria, which he suggested may represent an ancestral form leading to the genus *Sarcophilus*. The Smeaton site was considered by Gill (1957) to be pre-Holocene, either Pliocene or Pleistocene in age. On the other hand, Stirton (1957) suggested that if *Glaucodon* is in the direct line of ancestry of *Sarcophilus*, then the age of the Smeaton locality may be Miocene or even older. *Glaucodon* has recently been recorded from a late Pliocene or early Pleistocene locality along the Murray River, west of Mildura, New South Wales (Marshall, 1973), supporting a possible late Tertiary age for the Smeaton locality. This occurrence also suggests the contemporaneity of *Glaucodon* with the earliest *Sarcophilus*, recorded in 'Pliocene' sediments by De Vis (1883), McCoy (1882) and Stirton (1957). The present study deals with a redescription of *S. prior*, a re-evaluation of its taxonomic position and a re-examination of other specimens referred to *Sarcophilus* and assigned a 'Pliocene' age.

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Our special thanks are extended to Mr H. E. Wilkinson of the Victorian Geological Survey for drawing the authors' attention to the possible relationships of *S. prior* with the family Vombatidae and to Mr M. Archer of the Queensland Museum and Dr Richard H. Tedford of the American Museum of Natural History for valuable criticism.

Specimen numbers preceded by NMV are registered in the collections of the National Museum of Victoria, while those preceded by QM are housed in the Queensland Museum.

?*Vombatus prior* (De Vis, 1883)

(Pl. 26, figs. 1-5)

Sarcophilus prior De Vis, 1883, 187-90.

REVISED DESCRIPTION: Proximal end of right tibia, with maximum anterior posterior depth = 32.0 mm; maximum breadth = 29.0 mm; length from broken distal end of shaft to middle of intercondyloid eminence = 45.7 mm. The tibial tuberosity is broad and covered with rugosities dorsally. This surface dips ventrally at 45° relative to dorsal rim of medial condyle. The tibial crest is broad dorsally, narrowing slightly ventrally. The lateral fossa is relatively shallow. The medial condyle is larger than lateral and deeply basined dorsally. A shelf from the medial condyle extends posterolaterally behind base of intercondyloid eminence. The anterolateral and posterior edges of this eminence show breakage, although it does not appear as though much of the original surface is missing. The lateral condyle is relatively flat dorsally but its extent is reduced by breakage posteriorly and anterolaterally. Little of the posterior margin is believed missing and the lateral condyle did not extend greatly posterior to the intercondyloid eminence. The eminence is nipple-shaped and a small crest extends anteromedially to posterior edge of tibial tuberosity. The fibular facet is ovoid and situated on lateral face of lateral condyle. A sharp vertical cleft is present separating the median and lateral condyles, immediately posterior to intercondyloid eminence. Medial surface of shaft is flattened and a sharp rugose crest extends from medial edge of medial condyle ventrally onto posteromedial edge of shaft. The buttress below the medial condyle is only weakly developed.

DISCUSSION: ?*Vombatus prior* has been a *nomen dubium* since it was first described by De Vis (1883) within the genus *Sarcophilus*. The holotype, QM F743, the proximal end of an incomplete right tibia, was only briefly described by De Vis and comparison was made only with *S. ursinus* (= *S. harrisi*). Heavy mineralization and staining with oxides of iron suggest provenience with the late Pliocene Chinchilla Sand (Woods, 1956). Cranial remains of *Sarcophilus* have not been recorded from this Formation, but mandibular and maxillary specimens of other dasyurids, *Thylacinus* and the much smaller *Dasyurus*, have been recorded by Ride (1964) and Bartholomai (1971), respectively.

Compared with the living *S. harrisi* (NMV C6246, C6255 and QM J11282) there is a vertical furrow on the posteromedial surface of the shaft immediately below the medial condyle, a feature not seen in ?*V. prior*. The tibial tuberosity in *S. harrisi* has a pronounced anterolateral extension, while that in ?*V. prior* is markedly concave in this area

in proximal view. A distinct concavity appears dorsal to the lateral fossa. In addition, the fibular facet in *S. harrisii* faces more posteriad, not laterally as in ?*V. prior*. In actual size, *S. harrisii* is about one-third smaller.

In extant *Thylacinus* (NMV C5742 and C5741) the tibial fossa is deeper, the buttress below the lateral condyle is larger, the lateral condyle extends further posteriad and the cleft between the lateral and medial condyles is not as well defined as in ?*V. prior*. The fibular facet faces much more posteriad, while the proximal end of the tibia is proportionately deeper anterior posteriorly than in ?*V. prior*. There is a shelf from the medial condyle which extends posteriad to the intercondyloid eminence in both *Thylacinus* and *S. harrisii*, similar to that in ?*V. prior*, but both lack the posteromedial crest on the shaft below the medial condyle, seen in that species.

From the differences noted, it is apparent that the fossil tibia, QM F743, previously regarded as being referable to *Sarcophilus*, is markedly dissimilar to known larger dasyurids. Consideration of size is sufficient to exclude the extinct families Diprotodontidae and Thylacoleonidae in any re-assessment of the taxonomic position of the species, and in re-evaluating this position, only the families Vombatidae and Phascolarctidae need be compared, taking both size and morphology into account.

Phascolarctos (NMV C6728) has, however, a more convex medial surface, a smaller lateral fossa and a more anteriorly positioned lateral buttress.

Closest morphological comparisons in living marsupials are afforded by vombatids. ?*V. prior*, is similar to *Lasiorhinus* (NMV C6234, QM J9234 and QM J14051) in that the lateral buttress is poorly developed, the tibial tuberosity is broad and slopes sharply ventrally and the lateral condyle is short relative to the medial condyle. The intercondyloid eminence is longer antero-posteriorly in *Lasiorhinus latifrons* and *L. barnardi* and continues to the posterior edge of the medial condyle, lacking the shelving seen in ?*V. prior*. The fibular facet faces more posteriad. Measurements of the *Lasiorhinus latifrons* tibia (NMV C6234) are: maximum antero-posterior depth = 29.4 mm; maximum breadth = 29.2 mm. *L. barnardi* (QM J14051) corresponding dimensions are: 37.0 mm; 36.7 mm; these suggest a proportionately broader tibia than in ?*V. prior*.

In *Vombatus* (QM J10867) the lateral buttress is slightly better developed, the tibial tuberosity is only relatively slightly broader but both this genus and *Lasiorhinus* lack the posteromedial crest on the shaft below the medial condyle seen in ?*V. prior*. The intercondyloid eminence in *Vombatus* is more like that in *Lasiorhinus*. As in ?*V. prior*, however, the medial condyle is more shelf-like posterior to the eminence in *Vombatus*, while the fibular facet faces more laterally. Proportionately, the proximal end of the *Vombatus* tibia is more like that in ?*V. prior*. Measurements of the *Vombatus* tibia are: maximum antero-posterior depth = 35.8 mm; maximum breadth = 32.5 mm.

The evidence thus suggests that the tibia originally referred to *S. prior* shows closer affinities with the family Vombatidae than with other living and extinct marsupial families. Within the Vombatidae, a closer comparison is evident with *Vombatus* than *Lasiorhinus* among living forms. At present a number of fossil vombatids, apart from ?*V. prior*, are known in the Chinchilla Sand, including *Phascolonus*. Much of the post-cranial skeleton in *Phascolonus* has been described by Stirling (1913), including the tibia. Apart from size, this differs markedly in almost every detail in its morphology from ?*V. prior*. The post-

cranial skeleton in other fossil wombats is not well known and the present authors believe that reference of the species to ?*Vombatus* at this time is preferable to any alternative action which could be taken based on knowledge of other recognizable cranial remains in the late Pliocene Chinchilla Sand. *Vombatus* is recorded widely from the Pleistocene fluvial deposits of the eastern Darling Downs but cranial specimens have not yet been recorded from the Chinchilla Sand.

OTHER 'PLIOCENE' OCCURRENCES

McCoy (1882) reported *S. ursinus* (= *S. harrisii*) as abundant in the 'most recent Tertiary clays and in the various ossiferous caves of Victoria'. He referred to a specimen (NMV P7432, pl. 62, figs. 1-1b; and pl. 63, figs. 1-1d) collected from the 'Sandy beds intercalated with Pliocene Tertiary limestone near Queenscliff, in which the extinct Eared Seal, *Arctocephalus williamsi*, and the extinct wombat, *Phascolomys pliocenus*, occur'. These deposits are now recognized as no older than late Pleistocene and the specimen referred to as *A. williamsi* has been shown to be referable to the extant species *Neophoca cinerea* (Gill, 1968). The specimen figured by McCoy (1882) in pl. 61, fig. 5 (NMV P1857) was collected from a cave, five miles southeast of Gisborne (Gisborne Cave) and was found in association with the dingo, *Canis familiaris dingo*. Gisborne Cave as well as the contained fauna has been shown to be of a Holocene age (Gill, appendix in Mahoney, 1964). The above specimens fall well within the size range of the living *S. harrisii* from Tasmania (Table 1).

In the original description of *G. ballaratensis*, Stirton (1957) referred to a *Sarcophilus* collected from the 'Pliocene' at Kalamurina, from the Warburton River of northeastern South Australia. Stirton noted that this specimen showed a closer relationship to *S. laniarius* than to the living *S. harrisii*. Dr R. H. Tedford (pers. comm.) has informed us that the age of the Kalamurina locality has been reassessed and that further collections in this area have yielded a late Pleistocene *Diprotodon optatus* fauna. Stirton (1957) gave measurements of the specimen he referred to *Sarcophilus* showing that it was larger than the living species, *S. harrisii*, and slightly smaller than the specimen of *S. laniarius* with which he compared it. It is believed that this specimen could well prove referable to *S. laniarius*.

The genus *Sarcophilus* is represented by a single living species, *S. harrisii*, which survives today only in Tasmania. This species was reported as being present on the mainland from remains located in a midden at Tower Hill Beach, western Victoria, dated as recently as five centuries ago (Gill, 1953). This date has recently been amended by Gill (1971) and it has been shown that this site actually dates from about five thousand years ago. An extinct species, *S. laniarius*, is reported from late Pleistocene deposits throughout eastern Australia and Tasmania and, except for being larger in size, is indistinguishable from *S. harrisii*. A discussion of the distribution and relationships of these species is given by Calaby and White (1966). It is generally agreed that *S. laniarius* may be regarded as a larger ancestral form of *S. harrisii* (Calaby and White, 1966; Lydekker, 1887; Ride, 1964).

TABLE 1
POPULATION PARAMETERS FOR SOME CRANIAL AND MANDIBULAR CHARACTERS OF
A LIVING SAMPLE OF *Sarcophilus harrisii* FROM TASMANIA, COMPARED
WITH SPECIMENS OF HOLOCENE AGE FROM VICTORIA.

Tooth dimension	Living Specimens, Tasmania					Holocene, Victoria	
	N	O.R.	\bar{X}	s	V	NMV P7432	NMV P1857
P ¹ length	23	4.4- 5.5	4.84	0.292	6.03	4.5	—
max. width	23	4.4- 5.2	4.91	0.227	4.62	4.9	—
P ² length	27	6.0- 6.8	6.51	0.178	2.73	6.0	—
max. width	27	5.3- 6.4	5.80	0.228	3.93	5.7	—
M ¹ length	27	11.0-11.9	11.49	0.268	2.33	11.1	—
max. width	26	8.6- 9.7	9.23	0.281	3.04	9.0	—
M ² length	27	12.1-13.0	12.47	0.209	1.68	12.2	—
max. width	25	9.3-10.5	9.98	0.357	3.58	10.3	—
M ³ length	27	11.3-12.4	11.81	0.274	2.32	12.8	—
max. width	26	9.5-10.7	9.91	0.366	3.69	10.4	—
M ⁴ length	26	7.5- 9.0	8.34	0.448	5.37	7.9	—
max. width	26	3.4- 4.1	3.67	0.199	5.42	4.4	—
M ¹⁺³ length	27	33.4-36.1	35.04	0.635	1.81	35.4	—
P ₁ length	27	6.5- 7.4	6.93	0.231	3.33	6.4	—
max. width	27	4.0- 5.0	4.50	0.318	7.07	4.2	—
P ₂ length	27	6.5- 7.6	7.19	0.248	3.45	6.8	6.9
max. width	27	5.1- 6.0	5.66	0.275	4.86	5.7	5.5
M ₁ length	27	8.3- 9.3	9.00	0.245	2.72	8.8	8.5
max. width	27	6.0- 7.0	6.31	0.246	3.90	6.4	6.5
M ₂ length	27	10.0-10.6	10.19	0.183	1.80	10.0	9.5
max. width	27	6.2- 7.3	6.64	0.281	4.23	7.3	7.0
M ₃ length	27	11.2-12.4	11.59	0.276	2.38	11.1	11.0
max. width	27	6.4- 7.3	6.73	0.193	2.87	7.0	6.9
M ₄ length	27	10.7-12.2	11.46	0.441	3.85	11.3	11.0
max. width	26	5.9- 7.0	6.33	0.316	4.99	6.7	6.6
M ₁₋₄ length	27	39.7-42.8	41.30	0.880	2.13	40.3	39.8
Breadth of mandible ..							
below M ₃	27	9.3-11.8	10.34	0.677	6.55	10.3	10.3
Depth of mandible below M ₃	27	15.0-24.7	20.72	2.075	10.01	20.3	18.4

CONCLUSION

A reassignment of the holotype of *S. prior* within ?*Vombatus* and reinterpretations of previously reported 'Pliocene' occurrences of *Sarcophilus* show that there are no specimens of this genus which may be definitely assigned to a Pliocene age. *S. lanianus* is the earliest known representative of this genus and is presently recorded only from presumably late Pleistocene deposits. In line with this evidence, *Glaucodon*, as proposed by Stirton (1957), may be regarded as being in the direct line of ancestry to *Sarcophilus* and still come from deposits of a Pliocene-Pleistocene age, this age being supported by a late Pliocene occurrence of *Glaucodon* in Marshall (1973).

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PLATE 26

?*Vombatus prior* (De Vis, 1883)

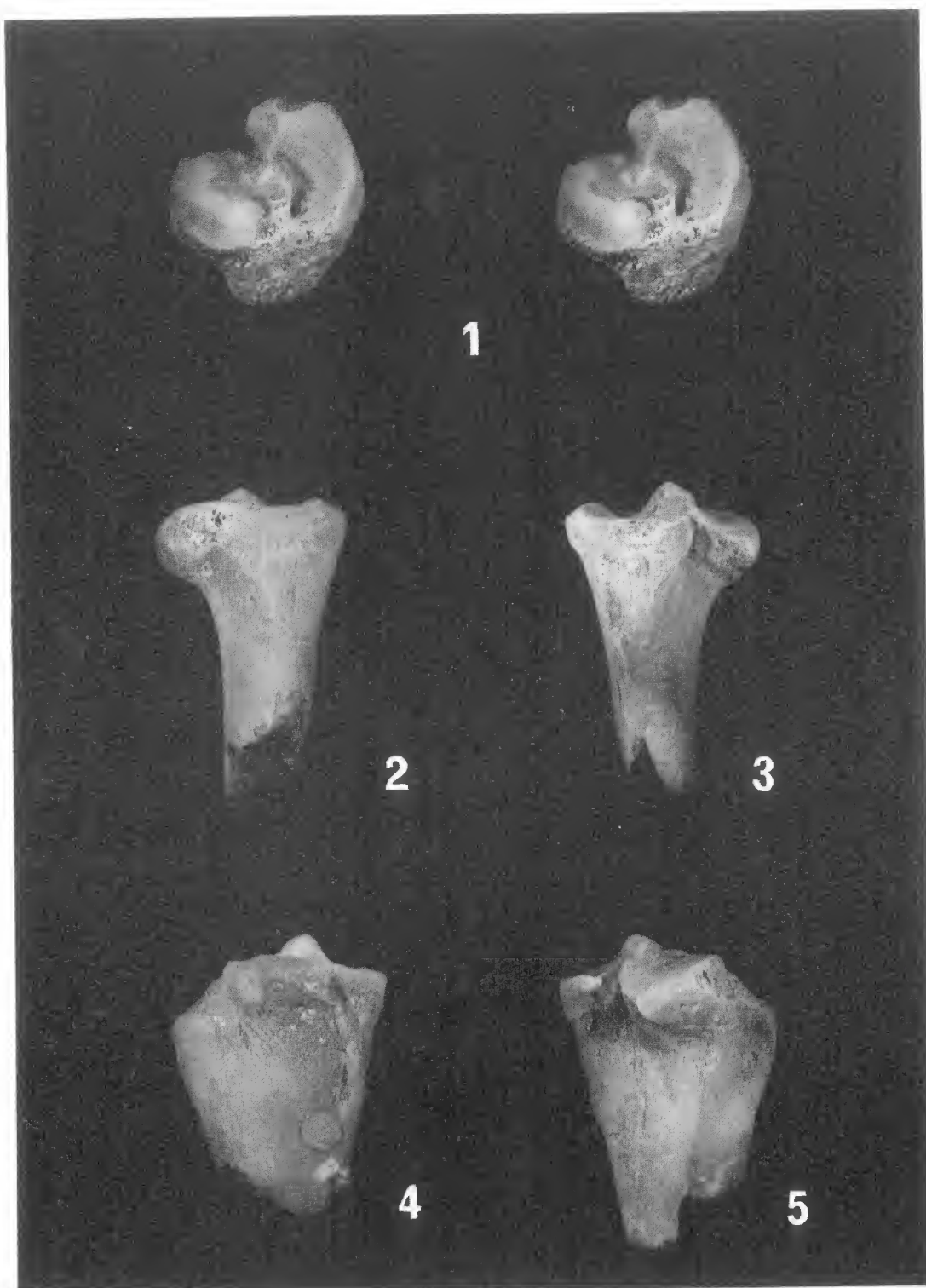
FIG. 1: Stereopair of proximal end of F743, holotype, ?Chinchilla Sand, western Darling Downs, $\times 1$.

FIG. 2: Anterior view of F743, $\times 1$.

FIG. 3: Posterior view of F743, $\times 1$.

FIG. 4: Mesial view of F743, $\times 1$.

FIG. 5: Lateral view of F743, $\times 1$.





THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 1.
THE BICOLOR GROUP

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ABSTRACT

A brief introduction to a systematic revision of the Australian lycosid spiders is given with a list of described species. Two new species *Lycosa forresti* and *Lycosa storri* are described with a review of the morphologically similar species *Lycosa bicolor*, *Lycosa errans*, *Lycosa castanea* and *Lycosa skeeti*. *Lycosa perinflata* is possibly a synonym of *Lycosa errans*.

The family Lycosidae, commonly known as Wolf Spiders, is almost cosmopolitan in its distribution. Within Australia this family is abundant in both species and numbers. At present some 113 species have been described. Rainbow (1911, pp. 264–76) provides references to 84 of these species; the remainder being described by Strand (1913), Rainbow (1915, 1917, 1920), Pulleine (1922), and Hickman (1944).

The writer commenced a systematic revision of the Australian species of the family Lycosidae in 1968. Shortly after, a large collection of Wolf Spiders was presented to the Western Australian Museum by Dr Barbara Y. Main, Zoology Department, University of Western Australia. This collection, in addition to Dr Main's notes on the type specimens held by the British Museum (Natural History), has proved of immense value to this investigation.

A number of personal surveys have been made throughout mainland Australia to gain information on the distribution, habitat selection, burrow construction, and life history of Wolf Spiders. The collections of other Australian museums and the type specimens from European museums are being examined.

MATERIALS AND METHODS

In this paper an effort has been made to reduce the technical terminology employed in the descriptions. Where this has been unavoidable the works of Comstock (1940), Main (1964), Hickman (1967), and Forster (1967) are useful references.

FIELD METHODS

COLLECTION. Wolf Spiders are largely nocturnal and although difficult to catch during the day, were readily collected at night with the aid of a head-torch.

BURROWS. These were exposed by digging a deeper hole adjacent to the burrow and the dimensions of the burrow recorded.

HABITAT. Topographical notes including degree of exposure, drainage, soil type, amount and composition of the litter, and notes on the surrounding vegetation were taken at the site of capture.

LIFE HISTORY. Information on the biology of each species was recorded whenever possible. This included records of seasonality, number and size of eggs laid, number of young released, food and feeding behaviour, and other natural history notes.

TAXONOMIC METHODS

MEASUREMENTS. All measurements were made on alcohol preserved material using a dial face 'Helios' caliper graduated in tenths of a millimetre, or by using a stereo dissecting microscope fitted with an ocular micrometer scale graduated in 100 units. The length of the carapace was taken along the midline, and leg segments were measured from articulation to articulation dorsally.

EYES. The eyes, disposed in three rows of 4, 2, 2, were referred to as anterior median eyes (AM), anterior lateral eyes (AL), posterior median eyes (PM) and posterior lateral eyes (PL). The ocular quadrangle included the eyes; the length and width was expressed in micrometer units. The ratio of the eyes was recorded as the maximum width of the separate eyes in micrometer units. A line tangential to the posterior margins of the anterior row of eyes (AM and AL) was curved anteriorly (procurved), straight, or curved posteriorly (recurved).

ILLUSTRATIONS. Drawings were from life, prepared from colour slides, or made with the assistance of a camera lucida or squared eyepiece graticule. The external surface of the epigynum was rubbed clear of hair and drawn in a dry condition. The internal genitalia were drawn from the dissected epigyna cleared in clove oil. In describing the genitalia the terminology of Bhatnagar and Sadana (1963) was followed. As the form of the epigynum of many species shows individual and geographic variation, a number of epigyna showing the internal genitalia as well as the external surface were illustrated for some of the species described. Published descriptions were not given in full; the serious student should consult the original descriptions if in doubt.

COLORATION. The colour descriptions were based on living specimens or on dried study material prepared by placing alcohol preserved specimens in 98% alcohol, 100% alcohol and xylene as described by Wallace (1942).

MATERIAL EXAMINED AND ABBREVIATIONS

Place names were those listed in the 'Gazetteer No. 40—Australia'. The following abbreviations were employed.

Collectors:

Mr A. Baynes	AB	Mr R. B. Humphries	RH
Mr W. H. Butler	HB	Dr Barbara Y. Main	BYM
Mr J. M. Gilbert	JG	Mr R. J. McKay	RJM

Institutions:

Australian Museum, New South Wales	AM
National Museum, Victoria	NM
Queensland Museum	QM
South Australian Museum	SAM
Western Australian Museum	WAM

Specimens:

mature specimens	M	juvenile specimens	J
penultimate instars	P	carapace length	C.L.

Family LYCOSIDAE

Ground dwelling spiders of small to quite large size. The eyes are characteristically arranged in three rows; the first row of four small eyes is located on the lower part of the face, frequently with the median pair larger than the laterals; the second row of two large eyes directed anteriorly; the third pair wider apart and located dorsally. The chelicerae have a robust basal segment (the paturon), with conspicuous lateral condyles, and a slender apical fang which lies at rest in a groove or cheliceral furrow, the margins of which bear teeth; the anterior or promarginal chelicerae teeth are usually three in number, with the median one largest; the posterior or retromarginal teeth vary from two to four, and are generally equal in size. The lorum of the pedicel of the abdomen is comprised of two pieces of which the posterior one is notched or recessed to receive the angular anterior one. The legs are long and frequently quite stout, the fourth pair longest. The distal margin of the trochanter has a notch on the ventral side. The females carry the egg cocoon attached to the spinnerets until the young hatch; the spiderlings, after hatching, clamber on to the abdomen and the posterior part of the carapace where they are carried by the female until the young disperse. For further information on the family the revision of the North American Lycosidae by Chamberlin (1908) can be consulted.

GENERA

A number of genera have been proposed in order to subdivide the large number of species included within the subfamily Lycosinae. Many genera are based on the relative size and spacing of the eyes, and the number of retromarginal cheliceral teeth. These characters have been found to be subject to some individual variation within some of the species examined by me. In compiling the following list of Australian lycosids I have

largely followed Guy (1966) in placing the species within accepted genera. I intend to review the Australian Wolf Spiders using Guy's generic boundaries until the Australian species are more adequately known, and then attempt a more natural classification. The first paper of this series describes a group of species I have termed the 'bicolor' group due to their similarity in coloration, form of the epigynum, and internal genitalia. A later regrouping of these species may result in their placement within the genus *Geolycosa* as a number of undescribed species with similar genitalia fall into the genera *Agalenocosa* and *Geolycosa*.

AUSTRALIAN SPECIES OF THE FAMILY LYCOSIDAE

CYCLOCTENINAE

<i>Cycloctenus</i> L. Koch, 1878	
<i>C. abyssinus</i> Urquhart, 1889	NSW
<i>C. flaviceps</i> L. Koch, 1878	Aust.
<i>C. vittatus</i> Rainbow, 1920	Lord Howe I.

HIPPASINAE

<i>Anomalomma</i> Simon, 1890	
<i>A. cinctipes</i> Simon, 1898	Qd
<i>Anomalosa</i> Roewer, 1960	
<i>A. kochi</i> (Simon, 1898)	Qd
<i>Venonia</i> Thorell, 1894	
<i>V. micarioides</i> (L. Koch, 1877)	Qd

PARDOSINAE

<i>Pardosa</i> C. L. Koch, 1848	
<i>P. eyrei</i> Hickman, 1944	SA
<i>P. pexa</i> Hickman, 1944	SA
<i>P. praevelox</i> Simon, 1909	WA
<i>P. versicolor</i> L. Koch, 1877	NSW
<i>Trabaea</i> Simon, 1876	
<i>T. lineata</i> L. Koch, 1877	NSW
<i>Trabaeola</i> Roewer, 1960	
<i>T. australiensis</i> (L. Koch, 1877)	NSW

LYCOSINAE

<i>Lycosa</i> Latreille, 1804	
<i>L. abmingani</i> Hickman, 1944	SA
<i>L. albopilata</i> Urquhart, 1893	Tas.
<i>L. aurea</i> Hogg, 1896	NT
<i>L. australicola</i> (Strand, 1913)	NT
<i>L. bicolor</i> Hogg, 1905	NT
<i>L. burti</i> Hickman, 1944	SA

<i>L. castanea</i> Hogg, 1905	SA
<i>L. celaenica</i> Rainbow, 1917	SA
<i>L. clara</i> L. Koch, 1877	Qd, NSW, Vic., SA
<i>L. cowlei</i> Hogg, 1896	NT
<i>L. dimota</i> Simon, 1909	WA
<i>L. errans</i> Hogg, 1905	SA
<i>L. excusor</i> L. Koch, 1867	Qd
<i>L. finkei</i> Hickman, 1944	SA
<i>L. flavisternis</i> L. Koch, 1877	Qd, NSW
<i>L. furcillata</i> L. Koch, 1867	Qd, NSW
<i>L. gilberta</i> Hogg, 1905	NSW
<i>L. gloriosa</i> Rainbow, 1920	Lord Howe I.
<i>L. habilis</i> (Hogg, 1905)	NSW
<i>L. halei</i> Hickman, 1944	NT
<i>L. hasseltii</i> L. Koch, 1877	Qd, SA
<i>L. hilaris</i> L. Koch, 1877	Tas.
<i>L. hostilis</i> L. Koch, 1877	Qd
<i>L. immansueta</i> Simon, 1909	WA
<i>L. impedita</i> Simon, 1909	WA
<i>L. inornata</i> L. Koch, 1877	Vic.
<i>L. lacertosa</i> L. Koch, 1877	SA
<i>L. laeta</i> L. Koch, 1877	Qd
<i>L. laeta curticeps</i> (Strand, 1913)	NT
<i>L. laeta protruda</i> (Strand, 1913)	NT
<i>L. marcentior</i> Simon, 1909	WA
<i>L. molyneuxi</i> Hogg, 1905	NSW
<i>L. naeviella</i> (Roewer, 1951)	NSW
<i>L. neptunus</i> (Rainbow, 1896)	NSW
<i>L. nigropunctata</i> Rainbow, 1915	SA
<i>L. obscuroides</i> (Strand, 1906)	Qd, NSW, SA, NT
<i>L. ornatula</i> L. Koch, 1877	Qd, NSW, Vic.
<i>L. palabunda</i> L. Koch, 1877	Qd, NSW
<i>L. percauta</i> Simon, 1909	WA
<i>L. perinflata</i> Pulleine, 1922	SA
<i>L. propitia</i> Simon, 1909	WA
<i>L. pruinosa</i> L. Koch, 1877	NSW
<i>L. pullastra</i> Simon, 1909	WA
<i>L. segregis</i> Simon, 1909	WA
<i>L. senilis</i> L. Koch, 1877	Qd, NSW
<i>L. sibyllina</i> Simon, 1909	WA
<i>L. simsoni</i> Simon, 1898	Tas.
<i>L. skeeti</i> Pulleine, 1922	SA
<i>L. speciosa</i> L. Koch, 1877	NSW
<i>L. spinipes</i> (Rainbow, 1896)	NSW

<i>L. subligata</i> (L. Koch, 1877)	Qd
<i>L. tasmanica</i> Hogg, 1905	Tas.
<i>L. tasmanicola</i> Roewer, 1960	Tas.
<i>L. topaziopsis</i> Hogg, 1896	SA
<i>L. tula</i> (Strand, 1913)	NT
<i>L. waitei</i> Rainbow, 1917	SA
<i>L. woodwardi</i> Simon, 1909	WA
<i>L. zualella</i> (Strand, 1907)	NSW
<i>Agalenocosa</i> Mello-Leitao, 1944	
<i>A. fallax</i> (L. Koch, 1877)	Qd
<i>A. leucophaeoides</i> (Roewer, 1951)	Qd, NT, Vic.
<i>Alopecosa</i> Simon, 1885	
<i>A. funesta</i> (C. L. Koch, 1837)	Tas.
<i>A. leonhardi</i> (Strand, 1913)	SA
<i>A. madigani</i> (Hickman, 1944)	NT
<i>Arctosa</i> C. L. Koch, 1848	
<i>A. goyderi</i> (Hickman, 1944)	SA
<i>Arkalosula</i> Roewer, 1954	
<i>A. semicincta</i> (L. Koch, 1877)	Qd
<i>Artoria</i> Thorell, 1877	
<i>A. cingulipes</i> Simon, 1909	WA
<i>A. flavimanus</i> Simon, 1909	WA
<i>A. taenifera</i> Simon, 1909	WA
<i>Cynosa</i> Caporiacco, 1933	
<i>C. ramosa</i> (L. Koch, 1877)	NSW, Vic.
<i>Diapontia</i> Keyserling, 1876	
<i>D. alboguttulata</i> (L. Koch, 1878)	Qd, NSW, Vic.
<i>Geolycosa</i> Montgomery, 1904	
<i>G. festina</i> (L. Koch, 1877)	Qd
<i>G. godeffroyi</i> (L. Koch, 1865)	NSW, Qd, Vic.
<i>G. pictiventris</i> (L. Koch, 1877)	NSW, Qd.
<i>G. serrata</i> (L. Koch, 1877)	NSW
<i>Hygrolycosa</i> Dahl, 1908	
<i>H. crispipes</i> (L. Koch, 1877)	Qd, NSW, NT
<i>Lycorma</i> Simon, 1885	
<i>L. albosparsa</i> (L. Koch, 1876)	Qd, NT
<i>L. bellatrix</i> (L. Koch, 1865)	Aust.
<i>L. subrufa</i> (Karsch, 1878)	Tas.
<i>L. meracula</i> (Simon, 1909)	WA
<i>Ocyale</i> Savigny and Audouin, 1825	
<i>O. oraria</i> (L. Koch, 1876)	WA
<i>Orinocosa</i> Chamberlin, 1916	
<i>O. stirlingae</i> (Hogg, 1905)	NSW

<i>Pirata</i> Sundevall, 1833	
<i>P. brisbanæ</i> (L. Koch, 1878)	Qd
<i>Schizocosa</i> Chamberlin, 1904	
<i>S. berenice</i> (L. Koch, 1877)	NSW, Vic.
<i>S. christopheri</i> (Simon, 1909)	WA
<i>S. egena</i> (L. Koch, 1877)	Qd
<i>S. expolita</i> (L. Koch, 1877)	Qd
<i>S. infensa</i> (L. Koch, 1877)	NSW, Qd
<i>S. leuckartii</i> (Thorell, 1870)	Qd, WA
<i>Tricca</i> Simon, 1898	
<i>T. phegeia</i> Simon, 1909	WA
<i>Trochosa</i> C. L. Koch, 1848	
<i>T. candicans</i> (L. Koch, 1877)	NSW, SA
<i>T. exculta</i> (L. Koch, 1876)	NSW
<i>T. martensii</i> (Karsch, 1878)	Aust.
<i>T. properipes</i> (Simon, 1909)	WA
<i>T. tristicula</i> (L. Koch, 1877)	NSW
<i>Varacosa</i> Chamberlin and Ivie, 1942	
<i>V. arenaris</i> (Hogg, 1905)	NT
<i>V. hickmani</i> Roewer, 1954	
(= <i>L. fletcheri</i> Hickman, 1944 preocc. Gravely, 1924)	NT
<i>V. phyllis</i> (Hogg, 1905)	NSW, SA
<i>V. pulveresparsa</i> (L. Koch, 1877)	Qd, NT
<i>Venator</i> Hogg, 1900	
<i>V. marginatus</i> Hogg, 1900	Vic.
<i>V. spenceri</i> Hogg, 1900	Vic.
<i>Venatrix</i> Roewer, 1954	
<i>V. fuscus</i> (Hogg, 1900)	Vic.

The following species described by F. Karsch in 1880 from the Hawaiian Islands are not Australian as listed by Roewer (1954).

<i>Lycosa aliusmodi</i>	<i>L. caduca</i>
<i>L. bruta</i>	<i>L. calvata</i>
<i>L. bruta filicum</i>	<i>L. virgata</i>

***Lycosa bicolor* Hogg, 1905**

(Figs. 1a-e, 2a-c)

Lycosa bicolor Hogg, 1905, pp. 580-2, fig. 85, no locality given; Rainbow, 1911, p. 266, Australia; Strand, 1913, p. 618, central Australia; Bonnet, 1957, p. 2636.

Allocosa bicolor: Roewer, 1954, p. 205.

MATERIAL EXAMINED

SYNTYPES: 3, SAM, labelled 'S.A. Mus. Coll. No locality—*Lycosa bicolor* Nov. Sp. H. R. H. Type' in pencil, '*Lycosa bicolor* Hogg. No locality. S.A. Museum coll.' in indian ink on separate labels, a small label in pencil, 'F. 194,' and 'Type' printed but badly faded. A lectotype is here designated from this series.

LECTOTYPE: ♀, C. L. 11.2 mm, epigynum fully developed, in good condition, separated from the syntype series with original labels. Appears to be the female illustrated by Hogg (1905, fig. 85b).

PARALECTOTYPES: ♀, C. L. 10.2 mm, epigynum small but completely formed, one leg and part of another leg missing. One ♂ P, C. L. 8.8 mm, abdomen and right legs detached.

OTHER MATERIAL: Western Australia: Burnabinmah Station, 25.v.1968, JG, WAM 69-92, WAM 71-880-1; Comet Vale, 20.v.1956, BYM, WAM 68-510; Cosmo Newbery 53 miles south, 21.v.1969, Christchurch School, WAM 69-841-2; Dales Gorge, Fortesque River, 29.ix.1969, RJM, A. Burbidge, WAM 69-1048; Great Northern Highway 482 mile peg, 24.v.1969, JG, WAM 69-878; Great Northern Highway 256 mile peg, 20.iv.1968, JG, WAM 69-891; Hammersley Gorge, Fortesque River, 29.ix.1969, RJM, WAM 69-1045; Jigalong, 1965, R. Kirkby, WAM 71-1438; Kangiangi, 26.i.1958, WAM 71-1436; Marvel Loch 28 miles southeast, 27-28, iii, 1969, J. Bannister, K. Youngson, WAM 69-668; Meekatharra 3 miles south, 1.x.1969, A. Burbidge, T. Evans, WAM 69-1049; Mount Bruce 18 miles west, 29.ix.1969, RJM, WAM 69-1046; Mount Bruce 13 miles east, 29.ix.1969, RJM, WAM 69-1047; Mount Gibson 2 miles east of turnoff, 7.xii.1968, RJM, JG WAM 68-792; Mount Gibson, 23.ii.1962, BYM, WAM 71-879; Mount Magnet 323 mile peg, 8.xii.1968, RJM, JG, WAM 68-822, WAM 69-843, WAM 69-877; Paynes Find 5 miles east, 28.ii.1970, RJM, WAM 70-55; Paynes Find 5 miles west, 10.iv.1955, BYM, WAM 68-506; Robe River area, 18.v.1971, Sampey Exploration Services, WAM 71-1439; Warburton Range, 1967-68, J. E. Carr, WAM 68-507-9, WAM 68-511, WAM 68-512, WAM 71-882-7; Warburton Mission, 3.ix.1963, M. de Graaf, WAM 69-836; Wubin, WAM 33-1613; Yandi, WAM 38-915.

Northern Territory: Ayres Rock, H. T. Phillips, WAM 68-513; Charlotte Waters, 1901-02, Spencer Gillen Expedition, NM; Ligertwood Cliffs 3 miles west, 21.v.1971, J. Dell, WAM 71-1437; Palm Creek, NM.

South Australia: Coober Pedy 10 miles east, 30.viii.1970, HB, W. D. L. Ride, WAM 70-214-6; Jay Creek, vi.1938, C. Barrett, SAM; Tallaringa Well 17 miles west, 13.iii.1970, J. Dell, WAM 70-50.

DESCRIPTION

Based on WAM 69-843, ♀, C. L. 10.2 mm.

Carapace uniform buff without lateral or median stripes. Abdomen intensely black above and below, with an anterior buff stripe longer than wide, pointed posteriorly, and extending to the middle of the abdomen. Sternum and coxae black. Legs black from coxae to near the extremities of the patellae above, and including the patellae below. Tibiae, tarsi and metatarsi buff. Labium and maxillae brown. Palps buff, with femora brown. Chelicerae with the anterior surface buff, becoming red-brown near fangs. Eyes frequently become emerald green in colour after preservation in alcohol.

Anterior row of eyes procurved, AM larger than AL, PM more than twice the diameter of the AM and 2/3 of their diameter apart. PL 3 diameters apart and about half that distance from the PM.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of equal size.

TABLE 1
MEASUREMENTS OF LEG SEGMENTS OF *L. bicolor* IN MM*

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	8.2	4.1	6.5	6.7	3.2
2	7.7	3.9	6.0	6.4	3.3
3	7.7	3.6	5.2	6.8	3.5
4	8.7	4.0	7.0	9.4	4.1
Palp	4.7	2.3	3.0	—	3.2

* WAM 69-1045, ♀M, C.L. 11.4 mm.

VARIATION: Juveniles are completely buff in colour with a slightly darker brown longitudinal lanceolate stripe on the anterior dorsal surface of the abdomen. The carapace is of a uniform buff colour with some examples having the area within the ocular quadrangle darker.

The transition to the adult coloration occurs at a C. L. of 6.4 to about 7.2 mm; the venter of the abdomen becomes black, and the anterior sides of the abdomen become dark brown to black; the femora are dark grey-brown to black and may be quite black in some small specimens; the undersurface of the femora usually becomes progressively darker until they are quite black. The black area of the venter extends up the lateral surface of the abdomen thus reducing the buff area of the dorsal surface until it almost disappears. Specimens from near Coober Pedy, S.A., have the carapace, the broad area on the dorsal surface of the abdomen, and the distal segments of the legs bright lemon-yellow. Adults show variation in the extent of the buff area on the dorsal surface of the abdomen, some examples are illustrated (Fig. 1 b-e).

The eye measurements were found to vary in the two specimens examined. ♀ P from Jay Creek, S.A., C.L. 9.3 mm, had the ratio of eyes AM:AL:PM:PL = 10:7:21:19; distance AM:AM 5, AM:AL 5, AM:PM 3.5, AL:PM 3, PM:PM 15. Clypeus to AM 7. Width of first eye row 46, width of second eye row 60. Ocular quadrangle 59×73 . WAM 69-1045, ♀ M, C.L. 11.4 mm, had ratio of eyes AM:AL:PM:PL = 15:9:35:27; distance AM:AM 7, AM:AL 6, AM:PM 4, AL:PM 4, PM:PM 20. Clypeus to AM 10. Width of first eye row 63, width of second eye row 80. The ratio of eyes given by Hogg (1905, fig. 85a) is AM:AL:PM:PL = 5:3:13:8.

The internal genitalia of two females is illustrated (Fig. 2 b, c). The epigynum of the lectotype is illustrated in Figure 2a.

SIZE RANGE: Mature females C.L. 9.1 to 12.0 mm.

DIAGNOSIS: *Lycosa bicolor* differs from the other members of the 'bicolor group', *L. forresti*, *L. storri*, *L. errans*, *L. castanea*, and *L. skeeti* in having the femora and half the patellae black and in having the abdomen completely black with an anterior dorsal longitudinal buff stripe of variable size.

LIFE HISTORY

Mature females are to be collected throughout the year, but are most common from September to March in W.A. Mature males are very rare and the palpal organ has not been described. Penultimate males have been collected from September to May, and appear to be most abundant in September in the Pilbara region of W.A. In the laboratory, females carry the egg cocoon attached to the spinnerets whilst in the burrow; in the field they have not been found, and it is possible that they completely seal the burrow during the period they are carrying the cocoon. One female carrying young was found occupying an open burrow near Mt Magnet, W.A., December 8, 1968; and by February at Paynes Find, juveniles in an early stage of transition to the adult coloration were very numerous.

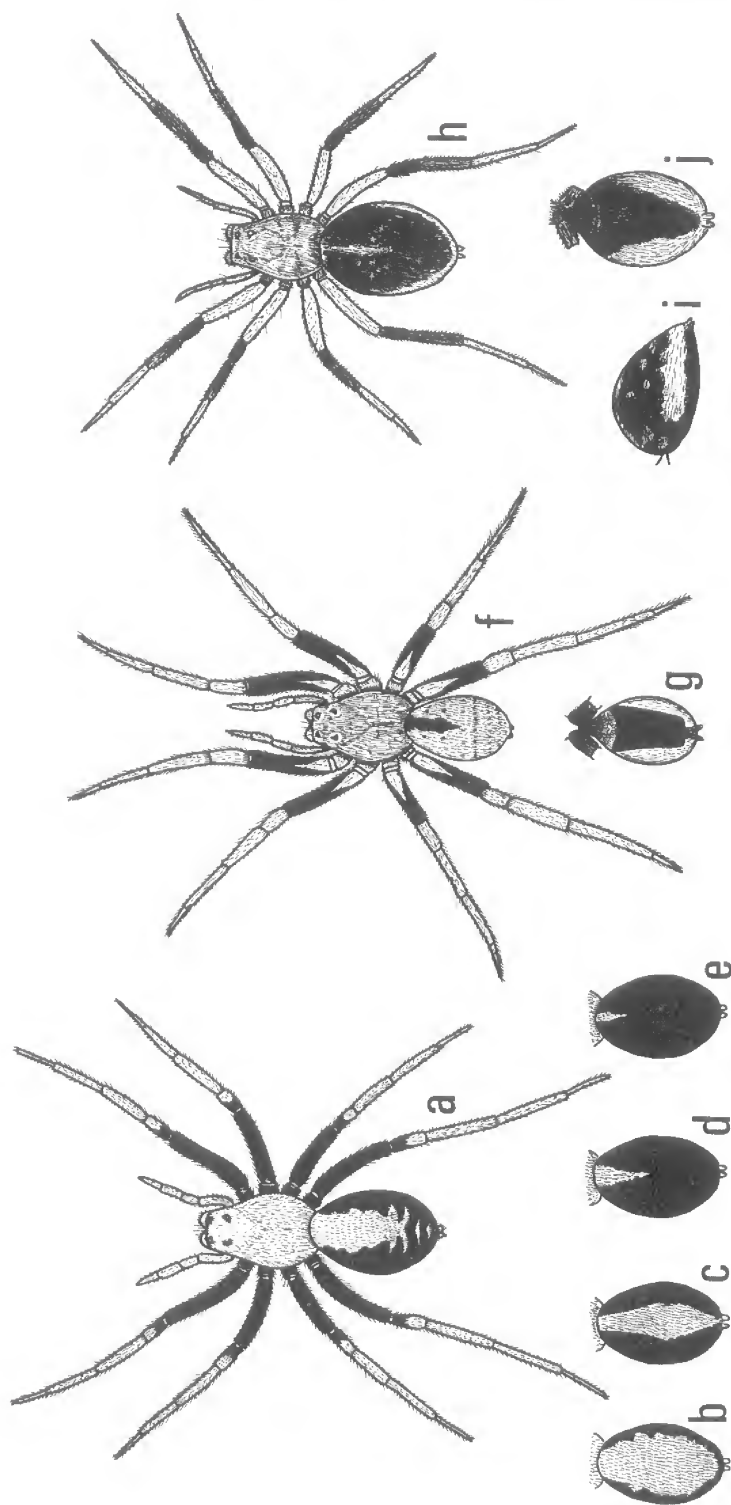


FIG. 1: a-e, *Lycosa bicolor*. a, mature female WAM 68-822, 323 mile peg, Mount Magnet, W.A.; b-e, dorsal surface of abdomen of WAM 69-1047, WAM 69-1046, 69-891, and WAM 68-507.
 f-g, *Lycosa forresti*. f, mature female WAM 69-456; g, ventral surface of abdomen.
 h-j, *Lycosa storri*. h, mature female WAM 68-828; i, lateral surface of abdomen; j, ventral surface of abdomen.

HABITAT

All specimens collected in Western Australia have been taken on 'arid red earth' or heavy 'desert loams'. The soil is frequently well compacted and may include red clay-loam, red-brown clay soil, and red earths associated with stone outcrops. A few specimens have been taken in the wind-swept heavy clay soils near desert sand-plain areas. Where road construction or clearing has disturbed the red clay-loams, *Lycosa bicolor* may take advantage of the more friable soil and construct burrows in the overturned areas. They have not been collected from sandy soils or from riverine alluvial soils. Vegetation is frequently Mulga *Acacia aneura*, *Eucalyptus* woodlands on red loams, and sometimes Mallee or *Triodia* on clay-loams. *Lycosa bicolor* is frequently taken in association with *Lycosa forresti* and *Lycosa storri*.

BURROW

The burrow is of an open vertical type without a trace of a mound or elevated rim. The burrow is usually constructed in open areas free from leaf litter or obstructing vegetation, and away from rocks, or *Triodia* tussocks. Burrows may descend to a depth of 23 cm in red loam soils or be as shallow as 10 cm in the more compact clay soils. The entrance is not sealed with a door or lid, but mature females may close the entrance with a thin web veil situated a few mm down the burrow. The diameter of the burrow depends on the size of the spider; a large female may have a burrow up to 16 mm in diameter. This species rarely leaves the burrow in search of prey, its characteristic position at night is just below the entrance, or half draped over the edge of the burrow. *Lycosa bicolor* retreats down the burrow when approached. The species is frequently aggressive when aroused, and may attack vigorously when first removed from the burrow.

In the laboratory, one large penultimate male was observed constructing a burrow in a glass aquarium three parts filled with red clay-loam. The excavated soil was loosely webbed into large pellets about the size of the abdomen, and carried to the far corner of the aquarium approximately 26 cm away, where it was piled against the glass. Some ten or more pellets were transported by the spider and dumped well away from the burrow; this enabled the burrow entrance to be maintained quite flush with the surface. Young females were observed to carry pellets of soil away from the burrow entrance, but mature females were reluctant to construct a burrow under laboratory conditions, and when they did so frequently deposited the soil nearby or in a mound surrounding the entrance.

DISTRIBUTION

South Australia, Northern Territory and Western Australia.

***Lycosa forresti* sp. nov.**

(Figs. 1f–g, 2d–g)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum WAM 70-44, ♀ M, C. L. 12.4 mm, 8 miles west of Moorine Rock, W.A., collected by Mr W. H. Butler, 8 January, 1970. In spirit.

PARATYPES: Western Australia; Buntine 3 miles southeast, ix. 1972, AB, N. Allen, 1 ♀ M, WAM 72-635, 2 ♀ M1J, WAM 72-639-41; Carrabin, 3.ix.1962, BYM, 1 ♀, WAM 69-37; Coonana 12 miles northwest, 25.i.1956, BYM, 1 ♀, WAM 69-35; Hyden, 26.i.1968, L. E. Koch, 1 ♂, WAM 69-801; Kulin, 1 ♀, WAM 33-1607; Lake

Moore near south end, 24.xi.1970, AB, 1 ♂ P, WAM 71-198; Laverton, 1 ♀, WAM 26-717; Marloo Station, 31.i.1968, L. E. Koch, 1 ♀, WAM 69-42; Marvel Loch 10 miles east-southeast at Neuoria Mine, 9.i.1970, HB, 1 ♀ M, WAM 70-30; Morawa, 17.viii.1953, BYM, 1 ♀ M, WAM 70-172; Paynes Find to Mount Magnet 323 mile peg, 7-8.xii.1968, RJM, JG, P. Snowball, 1 ♀, WAM 69-46, 1 ♂, WAM 69-465, 1 ♀ M, WAM 69-467, 1 ♀ M, WAM 69-791, 1 ♀ M, WAM 70-186; Rudall River, 5.v.1971, RJM, R. W. George, 1 ♀ M, WAM 71-1151; Southern Cross, 14.x.72, J. Bownds, 1 ♀ M, WAM 72-634; Southern Cross 6 miles east, 4.vi.1957, BYM, 1 ♀ M, WAM 69-40; Tammin, 28.viii.1956, BYM, 1 ♀, WAM 69-38; Wongan Hills 106 mile peg, 6.xii.1968, RJM, JG, 1 ♂ P, WAM 69-792; Wongan Hills to Ballidu 135 mile peg, 7.xii.1968, RJM, JG, P. Snowball, 1 ♀ M, WAM 69-827, 1 ♀ P, WAM 69-828; Wubin, 3.v.1963, J. Rayner, 1 ♀ P, WAM 69-41; Wubin 20 miles northeast, 14.vii.1968, RJM, JG, 1 ♀ J, WAM 69-43; Wubin 10 miles northeast, 14.vii.1968, RJM, JG, J. Ayres, 1 ♀ M, WAM 69-456; Yandi, 1 ♀ M, WAM 38-916 dried; Yellowdine 38 miles south, 6.xi.1970, HB, 1 ♀ M, 5 ♀ P, 1 ♂ P, WAM 71-69-75; Yellowdine 18 miles south, 23.x.1970, HB, 1 ♀ P, WAM 71-76.

DESCRIPTION

Based on the holotype.

Carapace uniform buff, without lateral or median stripes; head region around ocular quadrangle darker, face buff; some barely discernable radial furrows are present on the carapace, but these are not present in life; paturon black with the anterior surface buff; lateral condyle red; fangs black; labium and maxillae black; sternum black. Abdomen buff above and on sides; a jet black longitudinal lanceolate stripe on the anterior dorsal surface reaches to about middle of abdomen; on each side of this black stripe are scattered fine black spots becoming arranged into vague transverse rows posteriorly; venter with a broad black field reaching to and surrounding anterior spinnerets; region before epigastric furrow black. Legs with coxae and trochanters black ventrally, dorsal surface buff; femora jet black with wedge-shaped buff stripes on the proximal dorsal surface reaching to the middle of the femur; patellae black below, buff above, tibiae, metatarsi and tarsi buff above, dark grey below; palpi buff above, dark grey to black below; spines black.

Anterior row of eyes procurved, AM larger than AL, PM more than twice the diameter of the AM, and 2/3 of their diameter apart. Ratio of eyes AM:AL:PM:PL = 16:11:35:32; distance AM:AM 7, AM:AL 8, AM:PM 7, AL:PM 8, PM:PM 21. Clypeus to AM 17. Length of first eye row 69; length of second eye row 89.

TABLE 2
MEASUREMENTS OF LEG SEGMENTS OF *L. forresti* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1*	10.8	4.7	8.5	8.6	4.7
2*	10.0	4.5	7.5	8.3	5.0
3*	9.0	3.7	6.8	9.5	4.9
4*	11.0	4.5	9.0	12.5	5.3
Palp*	5.5	2.4	3.1	—	3.6
1†	11.1	4.1	8.8	9.0	4.6
2†	10.2	4.7	8.3	8.9	4.8
3†	9.2	4.6	7.2	9.7	5.3
4†	11.6	4.6	9.5	13.1	6.0
Palp†	5.5	2.7	3.2	—	4.0

* Holotype † WAM 71-69, ♀M, C.L. 12.8 mm

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of equal size (ten specimens examined).

VARIATION: Juveniles are buff with a pale brown, longitudinal, stripe on the anterior of the abdomen; a dull smoky grey to blackish longitudinal field on the venter of the abdomen. Some adults have the venter of the abdomen completely black, and lack the distinct lanceolate stripe on the anterior dorsal surface of the abdomen. It is possible that this species fragments into a number of separate populations, as the WAM collection contains atypical specimens from Forrest, Rawlinna, and the Fitzgerald River.

Eye measurements were recorded for 11 specimens; each measurement is given in Table 3 as a percent of the total width of the first eye row. Some variation is to be found in the eye proportions.

TABLE 3
EYE DIAMETERS AND INTERSPACES OF *L. forresti*
CONVERTED TO PERCENT OF THE TOTAL WIDTH OF
THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM
Holotype	♀M	12.4	23	16	51	46	10	12	30	10
WAM 72-635	♀M	11.7	23	16	48	45	9	9	35	10
WAM 72-639	J	7.7	22	17	50	45	9	7	30	9
WAM 72-640	♀M	12.5	25	15	52	46	9	6	30	10
WAM 72-641	♀M	12.4	24	17	51	43	9	7	33	9
WAM 70-30	♀M	12.7	25	15	49	44	9	9	32	10
WAM 70-172	♀M	12.4	25	15	52	45	9	7	33	10
WAM 72-634	♀M	13.5	23	15	48	44	10	8	37	11
WAM 69-827	♀M	11.3	23	15	48	46	9	8	32	9
WAM 71-69	♀M	13.2	24	15	51	43	8	7	32	8
WAM 71-70	♀P	11.0	24	16	52	44	10	7	35	8
WAM 71-71	♀P	9.9	24	15	51	44	10	7	29	10

The measurements of the leg segments also indicate variation in relative proportion of the separate segments as shown in Table 2.

Variation in the internal genitalia is shown in Figure 2 e-g. All mature females have the epigynum as illustrated in Figure 2d, the holotype was not figured.

SIZE RANGE: Mature females C.L. 10.3 to 13.8 mm.

DIAGNOSIS: *Lycosa forresti* may be distinguished by the presence of buff wedge-shaped areas on the femora, the coloration of the dorsal surface of the abdomen, and the presence of a strong lid closing the entrance of the burrow.

LIFE HISTORY: Mature females may be collected throughout the year, but appear to be most abundant during the summer months. Mature males have not been collected.

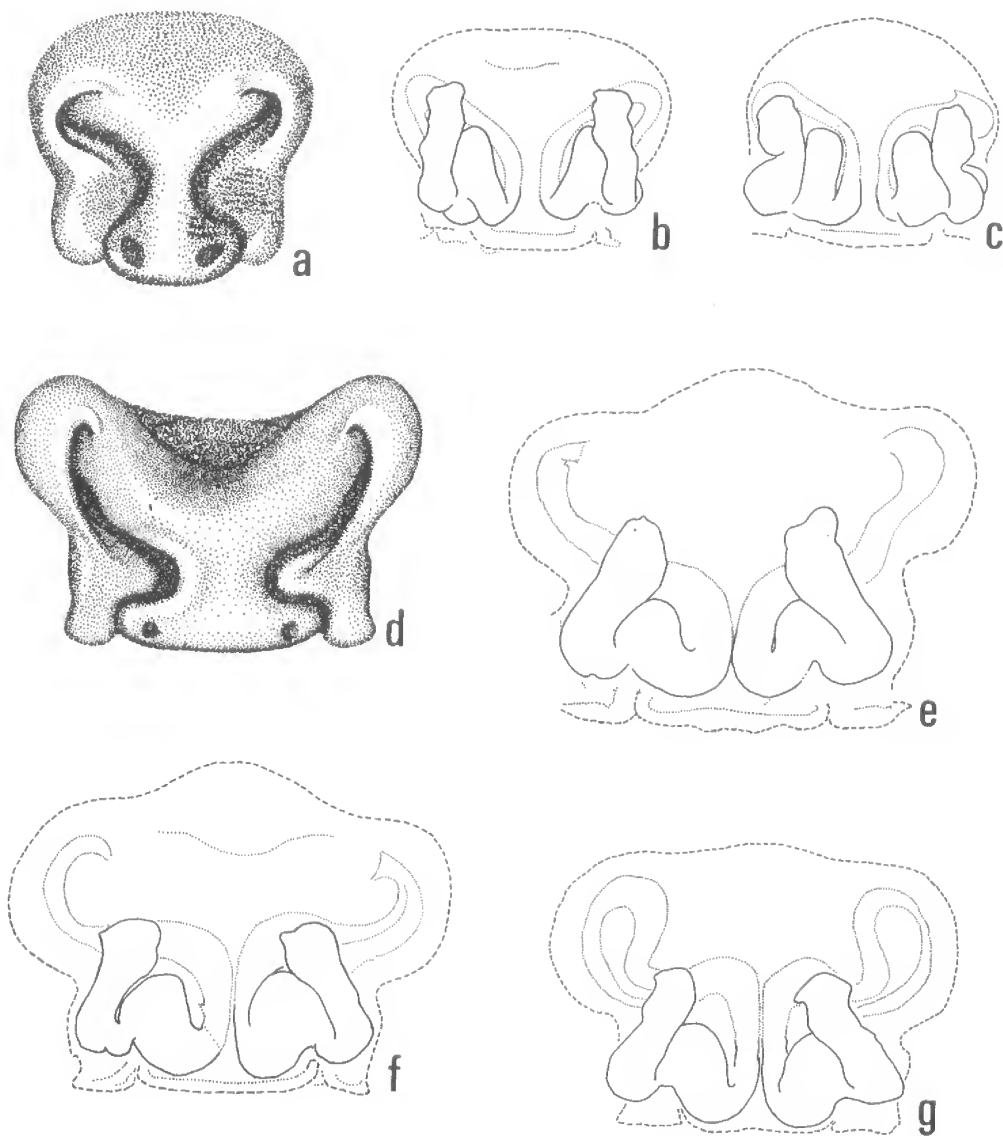


FIG. 2: a–c, *Lycosa bicolor*, female genitalia; a, epigynum of lectotype; b–c, internal genitalia of WAM 68-792, and WAM 69-1045.

d–g, *Lycosa forresti*, female genitalia; d, epigynum of WAM 69-35; e–g, internal genitalia of WAM 69-837, WAM 71-69, and WAM 69-827.

HABITAT

Red clay-loams with Mulga, Salmon Gum, and Spinifex. Some specimens have been collected from the margins of claypans by shaving the surface with a spade to expose the well concealed burrows.

BURROW

This species was thought to inhabit the heavy lidded burrows of mygalomorph spiders until burrows were constructed under laboratory conditions. The burrow extends to a depth of between 7 and 23 cm and has a maximum diameter of 17 mm. All burrows have a heavy silk-bound clay lid, tapered slightly to fit the entrance. When closed, the burrow is almost impossible to locate. On occasions the door may incorporate a piece of stone with a soil and silk cap. In the laboratory, females frequently seal the door shut with silk, and may remain within for a period exceeding one month; they can be induced to emerge by sprinkling water on the surface of the burrow area. The spider rarely leaves the burrow, and at night may be seen straddling the burrow with the hinged door thrown open. When disturbed, the spider rapidly retreats down the burrow pulling the door shut. If the door is gently prized open, the spider will attempt to pull the lid down from below by hooking the tarsal claws of the first pair of legs into the silk covering of the ventral surface of the door.

DISTRIBUTION

Arid and semi-arid regions of Western Australia.

DERIVATION

Named in honour of Sir John Forrest, Australian explorer, and first Premier of Western Australia.

***Lycosa storri* sp. nov.**

(Figs. 1h-j, 3a-e)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum WAM 70-240, ♀ M, C. L. 9.6 mm, 38 miles south of Yellowdine, W.A., collected by Mr W. H. Butler, 6 November, 1970. Epigynum removed but retained in tube. In spirit.

PARATYPES: Western Australia: Albion Downs 24 miles southwest, no date, BYM, 1 ♂ P, WAM 71-875; Billeranga, 15.viii.1953, BYM, 1 ♀, WAM 68-501; Broad Arrow, 4-8.iv.1969, B. Evans, 1 ♀ P, WAM 70-22; Burnabinmah Station, 25.v.1968, JG, 1 ♂ J, WAM 68-823, 1 ♀ M, WAM 68-828; Clinker Hill, 31.viii.1954, BYM, 1, WAM 68-504; Corrigin, 4.xi.1961, BYM, 1 ♀ M, WAM 71-874; Dulbellington, 29.ii.1957, BYM, 1J, WAM 68-825; Hyden, 10.vi.1952, BYM, 1 ♀ P, WAM 71-456, 29.iii.1954, BYM, 1J, WAM 69-884; Karonie 4 miles northeast, 25.i.1956, BYM, 1 ♀ M, WAM 68-505; Kellerberrin, 1938, 1 ♀, WAM 38-1298; Koorda, vii.1939, 1 ♀, WAM 39-2169, ii.1970, E. Hawkins, 1 ♀ M, WAM 70-245; Lake Moore near south end, 23-24.xi.1970, AB, 1 ♀ M, WAM 71-174, 1 ♀ M 1 ♂ P, WAM 71-175-6, 1J, WAM 71-197; Leonora 15 miles east, 18.vi.1969, L. E. Koch, D. D. Guiliani, 1J, WAM 70-206; Marloo Homestead, 31.1.1968, L. E. Koch, 1 ♀ M, WAM 69-835; Merredin, BYM, 1 ♀, WAM 68-502, 5.xii.1953, BYM, 1 ♀ M, WAM 69-888; Moorine Rock, 28.viii.1954, BYM, 1 ♀, WAM 68-500; Mount Gibson, 28.ii.1962, BYM, 1J, WAM 71-876, 1 ♀ M, WAM 71-877; Mullewa 1½ miles east, 19.iii.1957, BYM, 1 ♀ J, WAM 68-829; Muralgarra, 1939, 1 ♂ M, WAM 39-2564, 1 ♀ M, WAM 39-2565, 1 ♀ M, WAM 39-2566, dried specimens; Narembeen, 8.vi.1952, BYM, 1 ♀ M, 6 ♀ P, 5 ♀ J, 10 ♂ P, 10 J, WAM 69-962-94; Noongar, xi.1939, 1, WAM 39-2472; Nukarni, 1947, 1 ♀, WAM 47-963; Paynes Find

223 mile peg, 8.xii.1968, RJM, JG, 1 ♂, WAM 69-454; Paynes Find 5 miles east, 28.ii.1970, RJM, 2J, WAM 70-53-4, 4J, WAM 70-202-5; Quairading, 14.i.1954, BYM, 1, WAM 69-885; Randells 13 miles west on railway, 25.i.1956, BYM, 1 ♀ J, WAM 68-827; Walebing 3 miles north, 4.iv.1956, BYM, 1 ♀, WAM 68-498; Walyahmoning Rock 1 mile southwest, 31.v.1970, AB, 1, WAM 70-51; Warburton Range, 16.iii.1963, M. de Graaf, 1 ♀ M, WAM 71-878; Wialkie at Arnold's Water Reserve, 24.iv.1957, BYM, 1 ♀, WAM 68-826; Williams, 10.iv.1955, W. Sedgewick, 1 ♀, WAM 68-824; No locality, WAM 69-886, WAM 69-890, WAM 70-202.

DESCRIPTION

Based on the holotype.

Carapace buff, without lateral or median stripes; head region around ocular quad-angle almost black with buff hair, face dark; paturon black, fangs black; labium and maxillae dark brown; sternum dark brown; coxae and trochanters dark brown. Abdomen black with a thin continuous yellow-buff lateral band just before the spinnerets and continuing around the sides where it broadens until it reaches the middle of the abdomen; venter appears yellow from below with a black field from the epigastric furrow to the spinnerets, anterior to the epigastric furrow are pale yellowish areas; a faint narrow grey lanceolate stripe on the anterior dorsal surface reaching to about one third the length of the abdomen; spinnerets dark brown. Legs with femora bright yellow-buff with the dorsal surface pale brown; patellae and tibiae dark brown to black; metatarsi and tarsi yellowish-buff dorsally, darker below; spines black. Epigynum with the median arm of the guide broadest anteriorly (Fig. 3a).

TABLE 4
MEASUREMENTS OF LEG SEGMENTS OF *L. storri* IN MM.

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1*	7.4	2.9	5.4	5.6	3.3
2*	6.7	2.8	5.3	6.0	3.5
3*	6.4	2.8	4.2	6.1	3.5
4*	7.7	3.0	6.0	8.8	4.0
Palp*	3.9	1.6	2.3	—	2.8
1†	9.0	4.0	6.7	7.5	3.9
2†	8.2	3.8	6.1	7.5	4.0
3†	7.7	3.7	5.6	7.6	4.0
4†	9.2	4.0	7.3	10.1	4.8
Palp†	4.8	2.2	2.8	—	3.7
1‡	6.5	3.0	4.6	4.9	3.2
2‡	6.0	2.9	4.5	5.0	3.2
3‡	5.6	2.6	3.8	5.0	3.0
4‡	6.8	2.9	5.3	6.9	3.4
1**	7.3	3.0	5.2	5.4	3.1
2**	6.8	3.0	4.6	5.5	3.3
3**	6.0	2.9	4.2	5.6	3.4
4**	7.4	3.2	5.7	7.7	4.0

* Holotype † WAM 71-874, ♀M, C.L. 11.3 mm ‡ WAM 38-1298, ♀M, C.L. 8.5 mm

** WAM 39-2169, ♀, C.L. 9.2 mm

Anterior row of eyes procurved, AM much larger than AL. PM about $2\frac{1}{2}$ times the AM and $\frac{2}{3}$ of their diameter apart. Ratio of eyes AM:AL:PM:PL = 12:9:30:27; distance AM:AM 6, AM:AL 5, AM:PM 5, AL:PM 5, PM:PM 19. Clypeus to AM 10.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of equal size (thirty specimens examined).

VARIATION: Juveniles are completely buff in colour with a much darker red-brown longitudinal lanceolate stripe on the anterior dorsal surface of the abdomen. The juveniles are therefore very like those of *Lycosa bicolor*, but may be distinguished by the pronounced dark red-brown longitudinal stripe which reaches beyond the mid-length of the abdomen and may break up into a number of connected transverse chevrons. The transition to the adult coloration occurs at a C.L. of 4.0 to 7.0 mm; the venter of the abdomen has a somewhat triangular black field almost reaching the spinnerets; the anterolateral portion of the abdomen, and the dorsal surface, becomes dark-brown and then black; the patellae become dark-brown and then black, the femora remain yellow-buff. Juveniles of *Lycosa bicolor* at this size lack the pronounced dark red-brown markings on the dorsal surface of the abdomen, and when the patellae become dark brown, the distal halves of the femora are also very dark brown. Juveniles of both species may be found in adjacent burrows.

Adults show individual variation in the extent of the post-lateral yellow region of the abdomen; in some specimens this may continue forward and almost join anteriorly, in others this band may occupy most of the lateral surface, or be reduced to a narrow stripe. Adults normally have a narrow grey lanceolate stripe on the anterior dorsal surface of the abdomen, in some specimens this stripe may be absent in life but become conspicuous after preservation in alcohol.

Eye measurements were recorded for 10 specimens; each measurement is given below in Table 5 as a per-cent of the total width of the first eye row.

TABLE 5
EYE DIAMETERS AND INTERSPACES OF
L. storri CONVERTED TO PERCENT OF
THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM
Holotype	♀M	9.6	21	16	53	47	11	9	33	9
WAM 70-22	♀P	9.3	23	14	57	46	10	10	34	8
WAM 70-245	♀M	11.4	23	16	57	48	9	8	30	9
WAM 71-174	♀M	9.6	23	15	56	48	10	8	31	8
WAM 71-175	♀M	11.0	23	15	53	48	11	9	30	9
WAM 71-176	♀P	9.2	22	15	53	47	11	11	34	9
WAM 69-888	♀M	9.8	22	15	52	48	10	10	33	9
WAM 69-886	♀P	9.0	22	15	56	46	10	9	34	10
WAM 69-890	♀M	9.2	21	16	57	48	8	8	31	8
WAM 70-202	J	6.9	21	17	53	47	11	7	29	9

The measurements of the leg segments of 3 specimens are given in Table 4. Some variation in relative proportions can be observed.

The epigynum and internal genitalia of the holotype is illustrated in Figure 3a, e, with the internal genitalia of 3 additional females (WAM 70-245, WAM 69-962, WAM 69-888) illustrated in Figure 3b, c, d.

SIZE RANGE: Mature females C.L. 9.0 to 11.4 mm.

DIAGNOSIS: *Lycosa storri* belongs to the 'bicolor group' of species, but is readily identified by the yellow-buff femora, and the yellow or buff post-lateral area on the abdomen.

LIFE HISTORY

Mature females are to be collected from early November to February. Females carrying egg cocoons or young have not been observed, and it is not known when copulation takes place, as mature males are rare. During February the young are common in very small open burrows; by June the juveniles are in the transition stage to adult coloration. This species is commonly in association with *Lycosa bicolor*, a species with a very similar burrow, epigynum, and behaviour. The coloration of the legs is quite different however.

HABITAT

Red clay or red-brown desert loam soils with Mulga or Eucalyptus woodland. Some specimens have been reported from light sandy-loams of a yellow-brown colour (HB), on hard clay soil with a York Gum—Salmon Gum association (BYM), limestone desert soils with Mallee (BYM), or on red-pink soil at the bottom of a slope with *Acacia acuminata* and tussock grass (BYM).

BURROW

Open vertical type without a rim or mound, usually in open areas free of vegetation. The upper portion of the burrow is normally silk-lined and may on occasions be sealed with a thin webbed veil. The burrow has a maximum diameter of 16 mm and descends to a depth of between 13 and 20 cm. Some specimens have an enlarged terminal chamber up to twice the diameter of the burrow in width, and extending some 5 cm vertically. One specimen from Billeranga (WAM 68-501) was reported to have a pebble door (BYM). Juveniles may have a slight rim or mound at the entrance of the burrow whilst others have the burrow entrance flush with the surface. Under laboratory conditions females construct an open vertical burrow with a large chamber below.

Adults and juveniles drape the cephalothorax over the rim of the burrow, with the three anterior legs spread apart, and wait for prey to approach within range; the fourth pair of legs extend down the burrow with the posterior half of the abdomen. The spider rapidly withdraws itself down the burrow when disturbed. This species has not been observed to wander away from the burrow entrance.

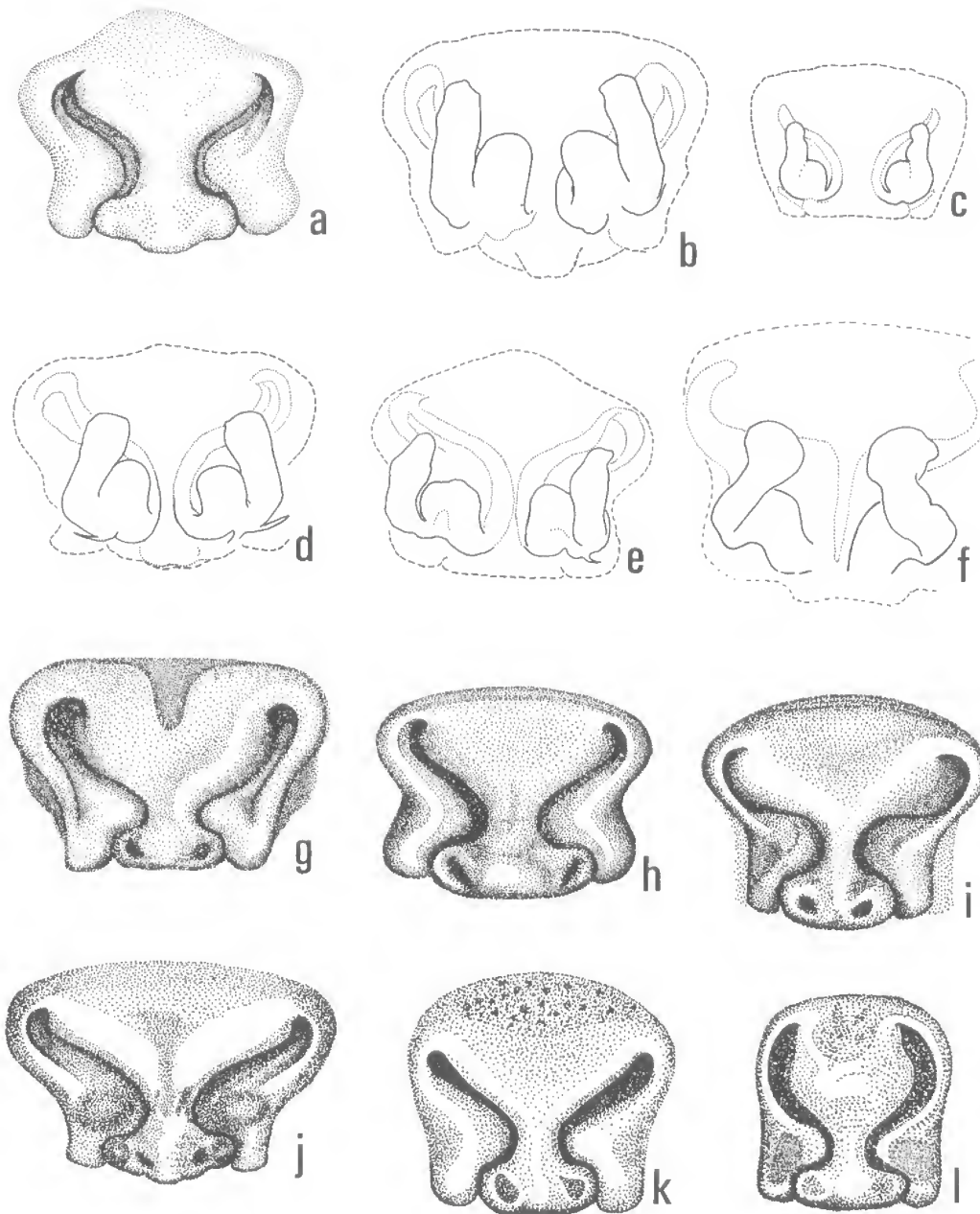


FIG. 3: a–e, *Lycosa storri*, female genitalia; a, epigynum of holotype; b–c, internal genitalia of WAM 70-245, WAM 69-962, WAM 69-888, and holotype.
 f–h, *Lycosa perinflata*, female genitalia; f, internal genitalia of WAM 71-643, g, epigynum of holotype; h, epigynum of female from Woolshed Flats, S.A.
 i, *Lycosa errans*, epigynum of holotype.
 j, *Lycosa castanea*, epigynum of holotype.
 k–l, *Lycosa skeeti*; k, epigynum of holotype; l, epigynum of female from Coopers Creek.

DISTRIBUTION

Arid and semi-arid regions of Western Australia.

DERIVATION

Named after Dr Glenn Storr of the Western Australian Museum in recognition of his taxonomic studies on Western Australian reptiles, and the encouragement he has given to taxonomists and naturalists.

***Lycosa errans* Hogg, 1905**

(Fig. 3i)

Lycosa errans Hogg, 1905, pp. 579–80, fig. 84, no locality given; Rainbow, 1911, p. 267; Bonnet, 1957, p. 2640.

Hoggicosa errans: Roewer, 1954, p. 247.

MATERIAL EXAMINED

HOLOTYPE: SAM, ♀ M, C. L. 12.6 mm, legs complete, labelled '*Lycosa errans*. H. R. Hogg. Type. No locality. F 170' in pencil, and on the reverse, 'S.A. Mus. Coll.'. One label '*Lycosa errans* Hogg. No locality' in indian ink, and 'Type' printed in orange. The holotype is in good condition, contrary to what Pulleine (1922, p. 83) states.

DESCRIPTION (After Hogg, 1905)

Female. Cephalothorax red-brown with yellow-brown hair; mandibles black-brown, with rather brighter coloured hair; labium, maxillae, sternum, and coxae dark chocolate-brown.

Abdomen dark brown above with four pale spots at the base, and transverse stripes of bright pale buff from middle to posterior end. Undersurface with a broad dark brown field reaching from base nearly to the spinnerets; sides light yellow-brown. Legs yellowish-brown, patellae and tibiae darkest, undersurface of the femora almost silver-grey.

Anterior row of eyes straight, the AL a radius from the AM which are $1\frac{1}{2}$ times that distance apart, their diameter being rather more than twice the same. AM a radius from the PM whose diameter is twice that of the AM and this is $1\frac{1}{2}$ times their distance apart.

Epigynum trapezoidal in outline, broadest anteriorly, where it is broader than its length.

Legs long and stout; no spines above on tibiae I and II; two each on tibiae III and IV.

DISCUSSION

Hogg (1905, p. 571) separates *Lycosa errans* from *Lycosa castanea* in his key to the species, and gives additional remarks under the discussion of *Lycosa castanea*. Unlike Hogg, I find two spines above on the tibiae of leg 2 in *L. errans*, and I find that the clypeus is about $\frac{3}{4}$ of the diameter of an AM in both holotypes (*L. errans* has clypeus 9–10 units, AM 14; *L. castanea* has clypeus 10, AM 14); the brown field on the venter of the holotype of *L. castanea* is slightly narrower than in *L. errans*. The ratio of the eyes of *L. errans* (holotype) AM:AL:PM:PL = 14:10:29:22; distance AM:AM 5, AM:AL 2.5, AM:PM 5, AL:PM 4, PM:PM 20. Width of anterior row of eyes 59.

The epigynum of the holotype has been poorly figured by Hogg (1905, fig. 84b) and is refigured here (Fig. 3i). Additional material may show that *Lycosa errans* and *Lycosa castanea* are synonyms. *Lycosa perinflata* is almost certainly a junior synonym of *Lycosa errans* but until more material becomes available I prefer to treat *L. perinflata* as a separate species.

DISTRIBUTION

South Australia.

Lycosa perinflata Pulleine, 1922

(Figs. 3f-h)

Lycosa perinflata Pulleine, 1922, p. 84, pl. 5, Whyte-Yarcowie, South Australia; Roewer, 1954, p. 272; Bonnet, 1957, p. 2657.

MATERIAL EXAMINED

HOLOTYPE: SAM, ♀ M, C. L. 11.9 mm, with all legs (except first on the left side, the femora and patellae of the fourth legs, and the left side palp) detached and loose within the tube. The skin has commenced to lift from the abdomen. Dark radiating lines are now visible on the carapace, and the colour pattern still persists on the abdomen.

OTHER MATERIAL: Woolshed Flats, S.A., iii.1908, R. H. Pulleine, ♀ M, C. L. 12.5 mm, SAM; Parachilna, S.A., 7 miles north, 22.viii.1970, HB, W. D. L. Ride, ♀ M, C. L. 13.4 mm, WAM 71-643.

DESCRIPTION (After Pulleine, 1922)

Female. Cephalothorax reddish-brown with fine white hair; median brown lines extending on to eye area in front, uniting behind and then spreading into a broad fork with radiating brown lines and spots on either side, running into a brown splashed area on the margins of the thorax; mandibles dark shining brown with thick white hair interspersed with dark brown hairs; labium and maxillae reddish brown; sternum and coxae darker brown with fine black hair.

Abdomen dirty white above with four discrete broad greyish-black bands interspersed with small spots, and a similar densely-spotted area on sides. Undersurface yellow-white with a broad longitudinal black band narrowing towards the black spinnerets.

Legs dark brown, undersurface of tibiae white in marked contrast to the remaining segments.

VARIATION: The eye measurements of the holotype are AM:AL:PM:PL = 13:9:29:22; distance AM:AM 5, AM:AL 2, AM:PM 5, AL:PM 3, PM:PM 16. Width of anterior row of eyes 53. The ♀ M from Woolshed Flats has AM:AL:PM:PL = 15:10:31:25; distance AM:AM 7, AM:AL 4, AM:PM 6, AL:PM 4, PM:PM 21. Ocular quadrangle 74 × 79. Clypeus to AM 11. Width of anterior row of eyes 62. WAM 71-643 has AM:AL:PM:PL = 18:13:43:35; distance AM:AM 9, AM:AL 4, AM:PM 8, AL:PM 8, PM:PM 25. Width of anterior row of eyes 78.

The chelicerae with three equal sized retromarginal teeth on each side; the left retromarginal teeth of the holotype have the inner two fused together at the base.

The epigyna of the holotype (Fig. 3g) and the female from Woolshed Flats (Fig. 3h) are illustrated. The internal genitalia of WAM 71-643 is shown in Figure 3f.

SIZE RANGE: Mature females C.L. 11.9 to 13.4.

DISCUSSION

A comparison of the holotypes of *Lycosa perinflata* and *Lycosa errans* leaves little doubt that *L. perinflata* is a junior synonym of *L. errans*. The illustration of the holotype of *L. errans* (Hogg, 1905, fig. 84a) is poor. WAM 71-643 has the colour pattern illustrated in Pulleine (1922, pl. 5).

BURROW

McKeown and Mincham (1948, pp. 214-5, 218) recorded this species from Willalo, S.A., and in this area counted fifty holes within a radius of two chains from a telephone pole. Apparently the burrows are open, vertical, and do not possess a lid or door.

DISTRIBUTION

South Australia.

***Lycosa castanea* Hogg, 1905**

(Fig. 3j)

Lycosa castanea Hogg, 1905, pp. 577-9, fig. 83, Adelaide, South Australia; Rainbow, 1911, p. 266; Bonnet, 1957, p. 2637.

Allocosa castanea: Roewer, 1954, p. 206.

MATERIAL EXAMINED

HOLOTYPE: SAM, ♀ M, C.L. 12.0 mm, labelled '*Lycosa castanea* H.R.H. S.A. Mus. No locality Type' in pencil, and '*Lycosa Castanea* Hogg. No Locality. S.A. Museum' on another label; included in the tube is a small label 'fig. 190' in pencil. Four legs are detached and loose within the tube; one leg has only the femur attached. The epigynum (Fig. 3j) is very similar to that of *Lycosa errans*.

DESCRIPTION (After Hogg, 1905)

Female. Cephalothorax and mandibles pale yellow-brown, with pale yellowish-grey hair; no distinct pattern; labium, maxillae, and coxae bright yellow-brown. Abdomen bright chestnut brown above with pale creamy-yellow transverse stripes. Undersurface with a chestnut triangular field, broadest at the base and narrowing to the spinnerets, which lie at its apex; sides pale creamy-yellow.

Anterior row of eyes straight, AM being $1\frac{1}{2}$ times as far apart as they are from the AL; their diameters are in the same proportion. AM a radius from the PM which are slightly less than their diameter apart and twice that of the AM. Clypeus as broad as the AM.

Epigynum of a trapezoidal outline, broader than long, with the broadest part anteriorly, where the middle ridge is also very broad, tapering to where it springs from a base of the usual type.

Legs long and powerful; one spine above on tibia I, two on tibiae II, III, and IV.

DISCUSSION

See discussion under *Lycosa errans*. Known only from the holotype.

DISTRIBUTION

South Australia.

Lycosa skeeti Pulleine, 1922

(Figs. 3k-1)

Lycosa skeeti Pulleine, 1922, pp. 83-4, pl. 5, Wilson, Flinders Range, South Australia; Roewer, 1954, p. 272; Bonnet, 1957, p. 2664.

MATERIAL EXAMINED

HOLOTYPE: SAM, ♀ M, C.L. about 13.7 mm, carapace badly broken on the thoracic part; abdomen shrunken; legs mostly broken off, but retained in tube; coloration as illustrated by Pulleine (1922, pl. 5). Two labels, '*Lycosa skeeti* Pulleine, Flinders Ranges, S.A., R.H.P. Coll. Wilson 4. 1908' in ink, and 'Wilson Sp. Ap. 08' in blue-green pencil. The epigynum is intact, and is now illustrated (Fig. 3k). I have labelled this specimen holotype.

OTHER MATERIAL: One ♀ M, C.L. 12.5 mm, SAM no date but labelled 'Pull. coll.' legs removed on one side and abdomen damaged; Coopers Creek, Pulleine coll., no date; ♀ P, C.L. 10.9 mm, SAM, ♀ M, C.L. 12.7 mm, SAM, epigynum well developed (Fig. 3l), both specimens are a little damaged but still have a pronounced and rather striking pattern on the dorsal surface of the abdomen; the ♀ P has a broad brown field almost covering the venter of the abdomen, reaching almost to the base of the spinnerets, the ♀ M has a narrower brown bar tapering slightly, and not reaching the base of the spinnerets.

DESCRIPTION (After Pulleine, 1922)

Female. Cephalothorax light brown, clothed with silvery-grey hair; darker brown median streak with four similar streaks on each side; mandibles with long silvery hair; labium, maxillae and sternum dark brown.

Abdomen light brown above, darker brownish-black below, with spinnerets a lighter shade: the dorsal surface of the abdomen has, on the posterior part, two nearly straight black parallel lines meeting at their ends; anterior to this, three black parallel sinuate lines; in front, two lateral black forked lines, not meeting medially.

Legs and palpi the same colour as the thorax and clothed with fine silvery hairs interspersed with strong black spines.

Epigynum small of simple form, i.e. two depressions with a median ridge.

DISCUSSION

Lycosa skeeti appears to be a valid species with a distinctive colour pattern. It is similar in many respects to *Lycosa bicolor* and may prove to be a subspecies of the latter.

Pulleine (1922, pl. 5) shows the femora to be much darker than the remaining leg segments although this is not mentioned in the description; the holotype has the femora dark brown. Additional specimens are required.

DISTRIBUTION

South Australia.

ACKNOWLEDGEMENTS

My thanks are due to the collectors listed above for their untiring efforts in the field. Mr John Gilbert of Western Australia is especially to be thanked for his enthusiastic assistance during many field trips, some of which were made at his expense. I am grateful to Mrs Hazel Udell for her carefully prepared colour illustrations copied by the author (Fig. 1). The illustrations of the external and internal epigyna were reproduced from the author's original pencil drawings by Mrs Cecily Fearnley.

Mr B. Campbell of the Queensland Museum offered valuable suggestions and criticisms of the manuscript, and Miss Jennifer Utz typed the final draft.

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A SHELL MIDDEN AT CASCADE GARDENS,
BROADBEACH, SOUTHEAST QUEENSLAND

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ABSTRACT

A rescue excavation of remnants of a shell midden at Cascade Gardens, Broadbeach, southeastern Queensland showed the site to be relatively recent and poor in anything but molluscan remains.

In mid 1970, the engineers supervising the widening of the Pacific Highway south of Cascade Gardens, Broadbeach, found that their work would destroy the remains of a typical Aboriginal shell midden. The Department of Main Roads immediately asked for the area to be inspected and evaluated by an archaeologist. This was done by M. C. Quinnell, who reported that there was some shell midden extant though much truncated and disturbed by earlier roadworks and local amateurs. Also, there were rumours that burials had been found in that area. The Aboriginal Relics Advisory Committee suggested that such a poorly preserved site did not warrant resumption but that it should not be destroyed without further archaeological investigation. Accordingly, it was decided that the site should be excavated as soon as possible with finance provided by the Department of Aboriginal and Island Affairs. L. Haglund-Calley was asked to direct and M. C. Quinnell acted as assistant. Equipment was provided by the Department of Anthropology and Sociology, University of Queensland, and the Department of Main Roads supplied transport and an office. The work force consisted of museum staff, Main Roads personnel, and volunteers from the Department of Anthropology and Sociology.

The excavation started on 20th July, 1970 and was completed on 26th July. We had then excavated three quarters of the extant midden and were convinced that we would learn no more by continuing. But we supervised the final clearing by machinery and satisfied ourselves that the excavated area was indeed representative.

This report is very much a co-operative effort. Thanks to specialists at the Queensland Museum who analyzed the faunal remains, what seemed a most unpromising site turned out to yield some interesting information.

SITE DESCRIPTION

The midden capped the remains of a sand dune on the eastern bank of the Little Tallebudgera Creek about 700 metres north of the junction between the Pacific Highway and the Nerang Road. (M.R. NP420000 *Burleigh*, Australia 1:50 000 map.)

The 350 and 400 cm contour lines (fig. 1) appeared to be mainly natural, in which case this dune was only a little longer—in a north to south direction—than it was broad, though part of a long stretch of dunes extending further to the north. Much disturbance had taken place, however, and it is likely that this affected the contours of the site to some extent. Judging from the outline of the remaining midden compared to the contours of the surrounding area and taking into account that this is frequently affected by flooding which can cover much of the slopes of the dune, it is unlikely that this patch of midden ever exceeded about 700 square metres. About 65 to 70 square metres remained when the excavation started. Rubbish pits and other disturbances had cut the midden on the western side. A fossicker's trench cut through what would once have been the centre of the midden. The area south of this had been destroyed or disturbed during earlier road making activities which also probably removed some midden on parts of the eastern slope. At the northern end the midden faded away naturally with the slope of the ground. There were also a number of rubbish pits in the remains of the midden, obviously modern and containing pennies, bottles and decaying shoes.

The midden was on the very edge of a mangrove swamp which follows the creek. To the east modern buildings have destroyed any natural vegetation, but the modern beach is only 500 metres away and the intervening area is not likely to have carried a very stable cover, judging from similar, but undeveloped areas nearby. A few large eucalypts were growing on the midden (Plate 27:a) as well as some young *Banksia* trees, but most of the area had been cleared by burning before the arrival of the archaeologists. The area to the north is now a picnic rest area and the natural vegetation has been turned into parkland. Areas within this are still covered by scattered shells, and it seems likely that this would have applied to the crests of most dunes in the area before modern development.

The shell deposits were not uniform in all parts of the site. On the eastern slope, towards the road (Fig. 1), we found three horizons of shell. The topmost (level 1A) was not in situ but material apparently pushed up by machines during road making. Below this, separated from it by a thin layer of pale sand, there were two horizons of shell (levels 1B:1 and 1B:2), both following the slope of the dune but separated by some pale sterile sand. They could be seen all along the slope but merged into one horizon in the highest part of the dune (lines M to P). This is what one could expect. Some shells near the slope of the dune would slide down and be covered by sand as soon as there was a strong east wind (Plate 27:b). The single horizon was between five and ten centimetres thick on the crest of the dune, containing whole or fragmented shells separated by pale to dark grey sand. Further west the horizon thickened, reaching a depth of about thirty

centimetres by lines T to V. Here the shells were very fragmented, closely packed and embedded in black sand with much charcoal (Plate 27:c). Clearly the western slope, though gentle, was favoured as a camping spot. The slope itself was not sufficient to give much protection from sea breezes but it is possible that the crest of the dune carried some sheltering vegetation.

The physical state of the shells varied somewhat but weathering had mainly affected the outer surfaces which were bleached and powdery. Somewhat less weathered and unbroken shells could sometimes, especially in the area L-P/15-20, be seen to underlie more weathered and broken ones, indicating that the difference was due more to the extent of exposure than to a difference in age.

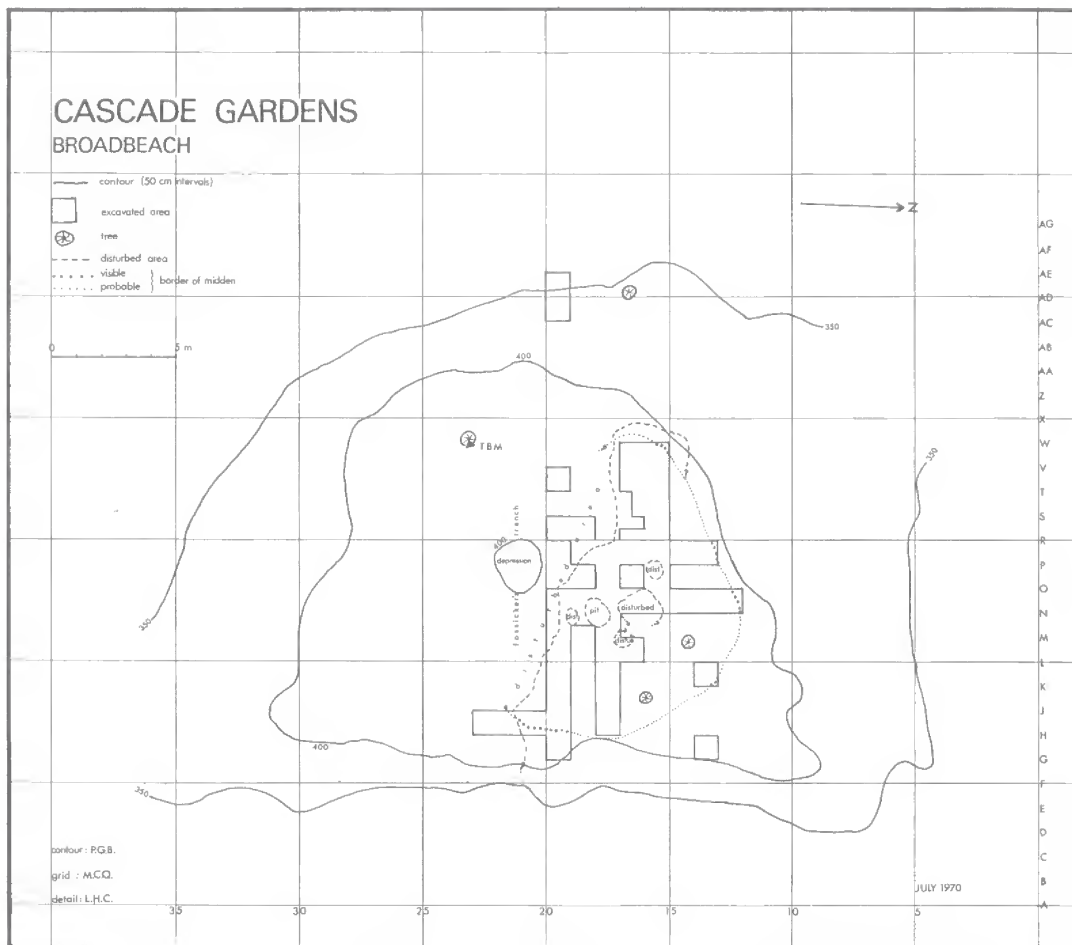


FIG. 1: Contour map of site.

THE FAUNAL CONTENT

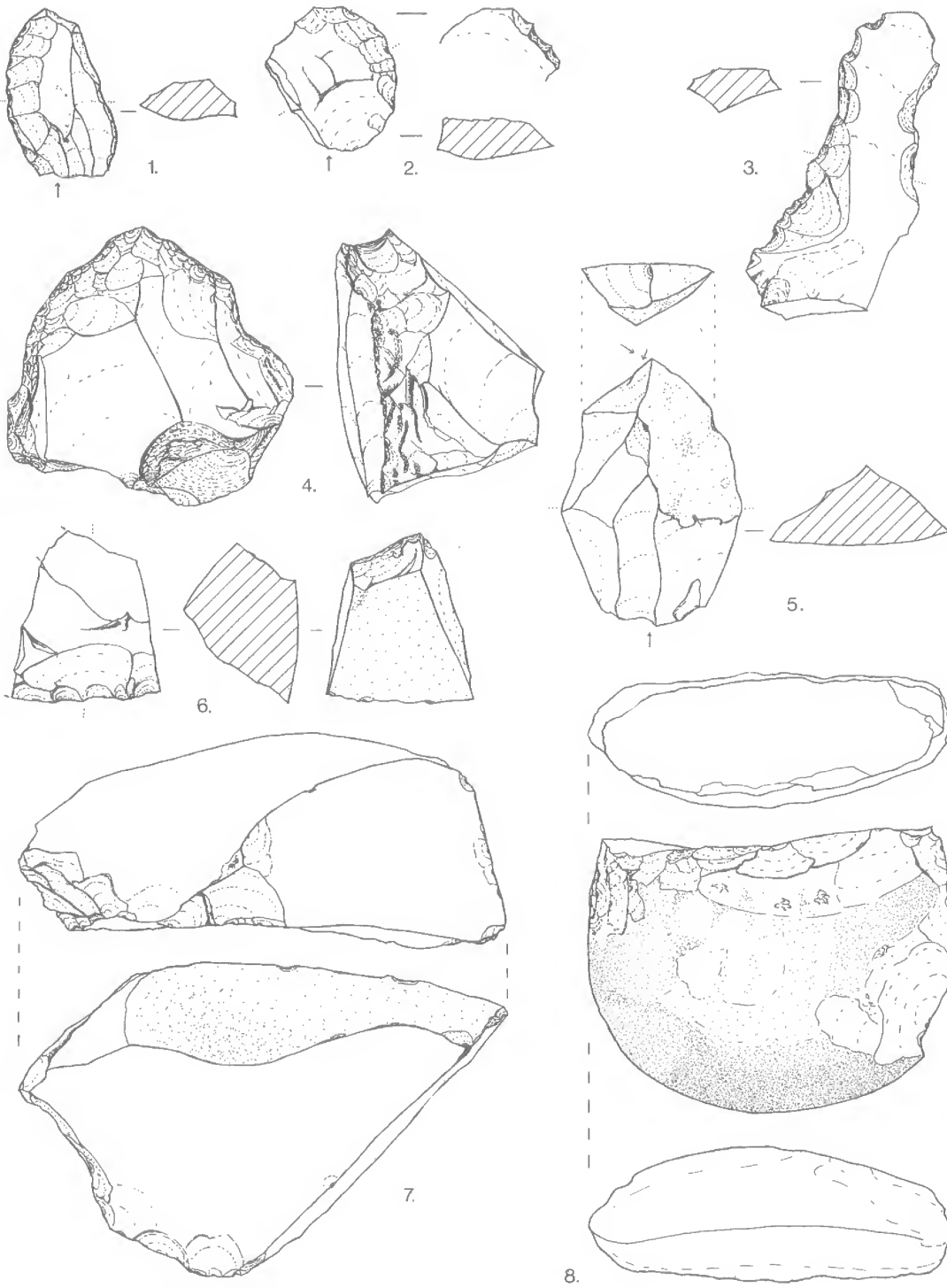
Faunal remains were found throughout the site, occurring in and above the midden deposit. The presence of these remains reflects the Aboriginal occupants exploitation of contiguous terrestrial, estuarine and marine environments for their food resources. The site, situated as it is, in close proximity to the estuarine conditions of Little Talleybudgera creek and the open ocean beach, was admirably suited to such a limited hunter-gatherer economy.

A wide range of land mammal and reptile species were collected (Appendix I) both from the coastal Wallum scrub in the vicinity of the site, e.g. bandicoot (*Isodon macrourus*) and bearded dragon (*Amphibolurus barbatus*); or ranging further afield, from the wet sclerophyll and closed forest of the Gold Coast hinterland, e.g. pademelon (*Thylogale* sp.). A small number of marine species, turtle (*Chelonia mydas* or *Caretta caretta*) and fish (unidentified) were also present. Mammal and reptile remains however formed only a small proportion of the total faunal content (14.75 kilograms by weight).

Discarded shells form the major portion of faunal remains at Cascade Gardens (Appendix II). The ocean beach intertidal yugari (*Plebidonax deltoides*) was the most dominant species present, comprising 99.7% of the total molluscan remains (by weight). Estuarine and tidal flat species such as *Pyrazus ebeninus* and *Anadara trapezia* were not present in significant numbers. This indicates a deliberate preferential choice on the part of the Aborigines in favour of the yugari as an article of diet. This species is present in a higher proportion than expected in terms of the relative availability of other molluscan populations in nearby habitats.

FIG. 2: Selected artefacts. Implements 1–6 are shown natural size, implements 7–8 are reduced to half natural size.

1. QE 9001-4 Chunky flake with oblique retouch (40–60°) and use-wear on the left margin, steep retouch = backing (71°) on the right. Size: 23 mm × 15 mm × 5 mm.
2. QE 9001-5 Chunky flake with oblique retouch (about 56°) on the right margin and distal end. Steep retouch (close to 90°) on part of left margin, the rest naturally thick. Size: 20 mm × 17 mm × 5 mm.
3. QE 9001-2 Oblong, oblique flake with inverse retouch on both margins. The angle of retouch forming serrations varies between 65–80°. Size: 44 mm × 25 mm × 7 mm.
4. QE 9001-1 Irregular core flaked from several directions and chipped or bruised from use. Size: 42 mm × 40 mm × 30 mm.
5. QE 9001-3 Burin? Chunky flake without retouch apart from two spalls at the distal end. Size: 38 mm × 25 mm × 7 mm.
6. QE 9001-10 Fragment of steep-scraper? Steep retouch (about 68°) from flat pebble face and similar retouch (at about 65–80°) from the opposite face. Size: 21 mm × 26 mm × 17 mm.
7. QE 9001-8 Pebble fragment. Two long rectangular faces meet in edge of about 60° which has been chipped by use. Two triangular faces meet in a flaked edge of about 60–85°, also chipped by use. Size: 133 mm × 69 mm × 93 mm.
8. QE 9001-7 Edge-ground axe. Angle of working edge 70–75°. Note slight twist. Flaked, pecked, ground and polished over most of the surface except deep flake-scars and pitting. Lenticular section. Apparently broken in half but chipped around the broken part thereafter. Size: 79 mm × 104 mm × 40 mm.



No quantification based on the estimated weight of edible flesh has been attempted. On such a basis the contribution of mammals and reptiles would be greater than is apparent from extant bone weight. However this would not alter the fact that at this site shellfish of one species were favoured as a food source.

Thus the land, estuary, and sea shore were all exploited, there being however a strong emphasis on the latter. Gathering as opposed to hunting was the major means of food collection. There is no evidence to indicate the role of plant food in the site, but it is worth noting that only few, and doubtful, grindstones were found. No specialized implements are required for collecting the yugari which can be dug from the sand with foot or hand. This may in part be the reason for the paucity of artefacts at this site.

No positive evidence was forthcoming to indicate whether the Aboriginal occupation at the Cascade Gardens midden was of a seasonal or permanent nature. A seasonal factor may account for the large proportion of an open beach molluscan species favoured over its estuarine counterparts, the non-appearance of certain land and marine mammals and reptiles, and the low lithic content.

THE LITHIC CONTENT

The quantity of stone excavated, 26.8 kilograms, was rather small in comparison to that of shells, giving a ratio of about 1 kilogram of stone to 30 kilograms of shell. Only a small proportion of this stone showed any clear signs of knapping or use, 1.3 kilograms being waste flakes and chips, and 2.5 kilograms being implements, cores, and hammerstones with much pitting from use. The remaining 23 kilograms consisted of fragments of pebbles, apparently broken by weathering rather than by use. Undoubted implements were few (12) and the larger ones usually broken (6). This would give the very low ratio of about 1 implement per 66 kilograms of shell. Some surface material could have been removed by amateur collectors and one local collector claimed to have removed several boxes of artefacts from the fossicker's trench across the site. We are inclined to treat this as a statement for political purposes rather than exactitude, since the clearly undisturbed parts of the midden were no richer in artefacts than other parts, and since this poverty of implements appears characteristic of archaeologically recent middens in this district (Haglund-Calley, in press).

The raw materials used were pebbles of igneous rocks, quartzites, and a very little chalcedonic silica. No petrological study has yet been made in Queensland of material from archaeological sites, but a visual inspection indicated that the raw materials are those commonly found in surface sites in the area. The quartzites and the chalcedonic silica are frequently characteristically coloured or patterned and can sometimes be sorted into groups likely to have been derived from one nodule or outcrop. It is at times possible to join several flakes and fragments to reconstitute part of the original core which strengthens the case for such groupings. Intersite comparisons are, however still uncertain.

Few implements were found and the range of types was limited. The recognizable types, whole or in fragments, are tabulated in Table 1.

TABLE 1
RANGE OF IMPLEMENT TYPES

Type	Total*
Core, irregular, cf. fig. 1:4	3
Core tool with use-polished edge	1 + (10)
Core tool with use-polished and chipped and bruised working edges	1 + (9)
Core tool with chipped and bruised working edges	(12)
Core tool with short chipped working edges transverse to long axis, cf. 'picks' and fig. 1:7	1
Grind stone?	(9)
Core tool with grinding surface plus chipped working edge	(3)
Steep scraper, cf. fig. 1:6	2
Burin?, cf. fig. 1:5	1?
Micro scraper, cf. fig. 1:1-2	2
Serrated flake, cf. fig. 1:3	1
Ground edge axe, cf. fig. 1:8	1 + (5)

* Fragments constituting less than half the original artefact are quoted within brackets.

Unmodified waste flakes more than 10 millimetres long were measured in terms of greatest length in the direction of the detaching blow, greatest width at right angles to this, greatest thickness, and angle of striking platform. The results are shown as histograms in Fig. 3. The sample is very small, but since the histograms agree very closely with those resulting from the analysis of about 1300 waste flakes from a site nearby (Haglund-Calley, in press) it is likely that they do in fact reflect the technological tradition of the area during a certain period.

There was also a quantity of haematite in the site as well as some white devitrified chalcedonic silica which, being very powdery and soft, could also be interpreted as a pigment. The haematite occurred as soft crumbs, usually brick red, and as small lumps, harder and darker red, with one or more facets of polish suggesting that they had been rubbed against something hard and smooth, such as bone or wood. Since there was no evidence whatsoever that the site had been used as a burial ground the pigment must have been used on living bodies or artefacts as is still done in groups further north leading a traditional way of life (cf. Haglund-Calley, 1968).

DATING

The site contained a quantity of charcoal, but most, or possibly all, is likely to be contaminated. We found parts of the site still saturated with diesel oil which had been used to start the fire clearing the area. Though we could locate the worst spots by smell there is no guarantee that other areas had not been affected to some extent. Some samples of charcoal taken from the lower horizon of shells (level 1B:2) on the eastern slope may be useful, having been covered with a considerably thicker layer of deposit and so being more protected, but it has not been considered worthwhile to test samples of such doubtful quality when other types of evidence indicate that the site is late in terms of Australian prehistory.

The geological formation underneath the site is not likely to date back more than 2–3000 years (Coaldrake, 1962; Gardner, 1955). The cultural deposit was thin and but thinly covered with sand and humus. The shells had not had time to weather badly even where the shell layer was thin and the action of rain water plus dissolved chemicals from the layer of humus would have had most effect. The meagre artefact content would not look out of place if added to that of the Broadbeach burial ground nearby which is securely dated to the last millenium before present. Bones of a turtle found near the surface but in undisturbed parts of the midden and clearly part of the cultural layer, had been cut with a thin metal saw of the type butchers still use, cf. Plate 27:d. A jaw fragment of the European hare was found in an undisturbed part of the midden which indicates that the camp site was in use well after 1870 (see Appendix I). This would be quite possible since, according to reliable sources (Lenz, undated), groups of natives were still wandering in the Nerang area as late as 1884.

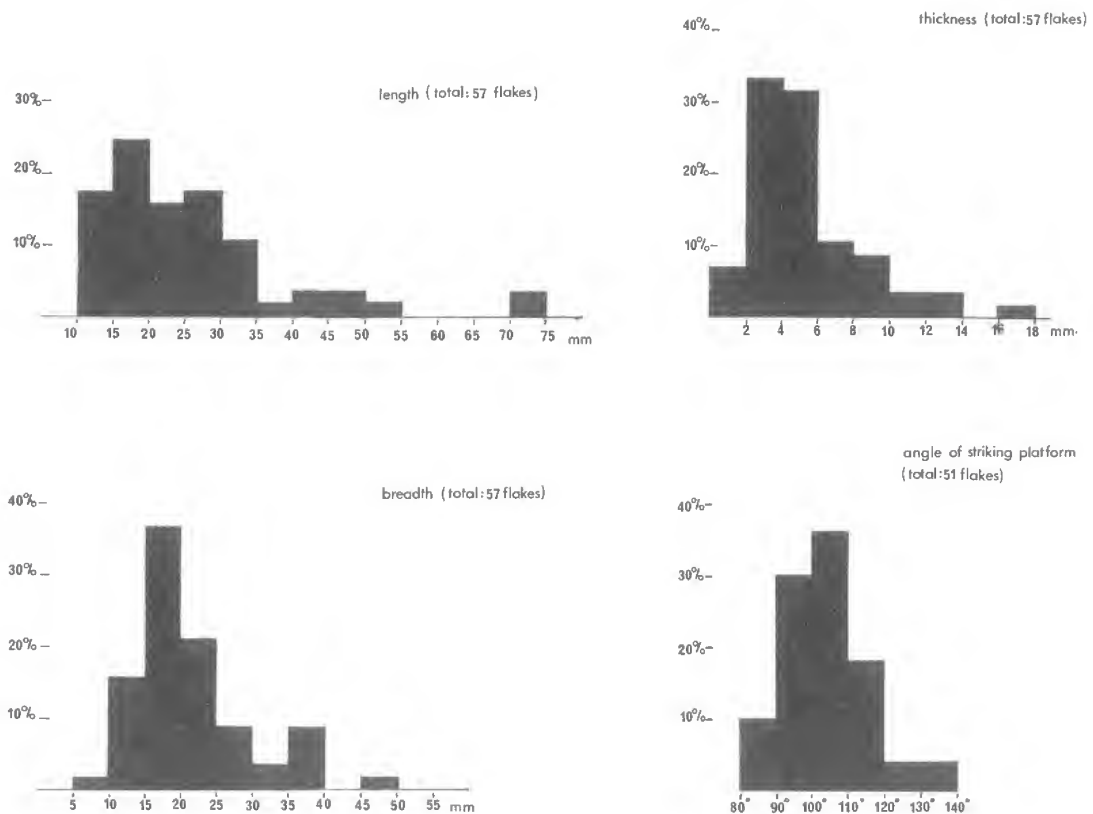


FIG. 3: Histograms showing the characteristics of waste flakes from the midden at Cascade Gardens.

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APPENDIX I

THE REPTILE AND MAMMAL REMAINS

Many of the remains are post-cranial fragments which cannot be identified positively but identifiable bones from the following species are present.

REPTILIA

- Chelydidae
 - Tortoise *Emydura* sp., possibly *Chelodina* sp.
- Cheloniidae
 - Turtle *Chelonia mydas* or *Caretta caretta*
- Agamidae
 - Bearded Dragon *Amphibolurus barbatus*
- Varanidae
 - Goanna *Varanus* sp. probably *V. varius*

MAMMALIA

- Peramelidae
 - Short-nosed Bandicoot *Isodon macrourus*
- Phalangeridae
 - Ring-tail Possum *Pseudocheirus peregrinus*
 - Brush-tail Possum *Trichosurus vulpecula*
- Macropodidae
 - Pademelon *Thylogale* sp.
 - Wallaby *Macropus* sp., probably *M. rufogrisae*
 - Swamp Wallaby *Wallabia bicolor*
- Muridae
 - Swamp Rat *Rattus lutreolus*
 - Rat *Rattus* sp., probably *fuscipes*
- Leporidae
 - European Hare *Lepus europaeus*

All are common in coastal southeastern Queensland today and most undoubtedly occurred at or very close to the camp site prior to and during early white settlement of the area. Several species are still found in the 'Cascade Gardens' Park which has been established on the site. Bearded Dragons, Lace Monitors, Bandicoots and Brush-tailed Possums have been observed there recently (March–May, 1969) and most of the others occur

within 8km of the site wherever suitable habitats have been preserved. Green and Loggerhead Turtles are common in Moreton Bay and are often seen in the Southport basin.

The remains of Pademelons, a Swamp Rat, and a European Hare are of special interest.

Pademelons, *Thylogale stigmatica* and *T. thetis* are usually confined to close and adjoining wet sclerophyll forests in southeastern Queensland. The camp site is in a sandy area which supported coastal wallum plant communities before 'civilization', so it seems reasonable to assume that the Pademelons had been hunted some distance from the camp. Closed and wet sclerophyll forest in which both species abound cover the Gold Coast hinterland except for cleared areas, and there is an isolated stand of closed forest in which a small population of *T. stigmatica* survives, in the Burleigh Heads National Park (B. Cook, pers. comm.) which is approximately 9.6 km from the site.

Rattus lutreolus is poorly represented in the Museum reference collection, probably because it is more difficult to trap than most other *Rattus* species, so its distribution in southeastern Queensland is uncertain. It is common on North Stradbroke Island and probably occurs on South Stradbroke Island although no survey work has been done on the latter. These Islands were a continuum until 1896 (Welsby, 1967, p. 331). *R. lutreolus* has been trapped in many other localities close to the camp site—Burleigh Heads, Lamington National Park, Mt Tamborine—so this species probably occurred throughout the coastal area in suitable habitats including the camp site.

The European Hare was brought into Australia (to Victoria) in 1870–71. (Troughton, 1941, p. 260). It is possible that the jaw bone found is more recent than the other skeletal material but, if not, its presence may be of use in dating the site.

Many reptiles and mammals which presumably would be suitable as a food source and are very common in the camp site area are not represented in the remains. It would not have been surprising to have found remains of the Blue-tongue Lizard (*Tiliqua scincoides*), Carpet Snake (*Morelia spilotes variegata*), Dugong (*Dugong dugon*), and the Common Dolphin (*Sotalia godami*) among others.

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APPENDIX II

THE MOLLUSCAN REMAINS

The midden was situated in close proximity to both estuarine and ocean beach environments, the former being more readily accessible. Molluscs represented in the midden sample included species characteristic of both habitat types.

Estuarine or tidal flat species:

Pyrazus ebeninus (Brugiere, 1792)

Crassostrea commercialis (Iredale and Roughley, 1953)

Regozara flava (Linne, 1758)

Anadara trapezia (Deshayes, 1840)

Ocean beach species:

Plebidonax deltoides (Lamarck, 1818)

Two species, *Polinices incei* (Philippi, 1851) and *Polinices conicus* (Lamarck, 1822), common to both environments, and a land pulmonate *Sphaerospira fraseri* (Griffith and Pidgeon, 1833) were also recorded.

Species composition of the sample was estimated in terms of relative proportions by weight.

Species	Weight in gms.
<i>Plebidonax deltoides</i>	185,594
<i>Pyrasmus ebeninus</i>	1,698.2
<i>Polinices incei</i>	687.4
<i>Crassostrea commercialis</i>	61.75
* <i>Regozara flava</i>	16.1
<i>Anadara trapezia</i>	14.75
† <i>Polinices conicus</i>	4.8
† <i>Sphaerospira fraseri</i>	5.7

* represented by fragments.

† represented by a single specimen.

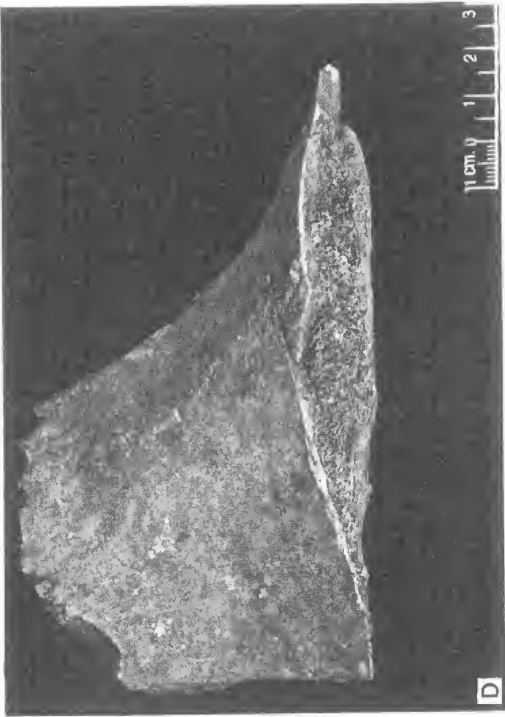
The shell midden could be considered as an artificial sample of the local mollusc fauna. Detailed ecological studies of both ocean beach and estuarine environments in southeast Queensland have yet to be conducted, however Dakin (1963) considered all marine species here represented to be 'common' in similar New South Wales intertidal areas. If food species selection was random, the midden sample would be expected to contain each species in a proportion relative to its local abundance. Results show, however, that the observed contribution of the Yugari, *Plebidonax deltoides* (in terms of shell weight) in the sample far exceeded its expected proportion indicating that this species was preferentially collected and was the dominant mollusc food species.

Helen M. King
Queensland Museum

DAKIN, W. J., 1963. Mollusca. In 'Australian Seashores' (Angus and Robertson: Sydney)

PLATE 27

- A. The midden surface cleared by burning.
- B. Two horizons of shell on the eastern slope.
- C. Thick deposit of food debris, ash and charcoal on the western slope.
- D. Note clean cut by metal saw. The turtle bones came from an undisturbed part of the midden deposit.





THE COURTSHIP BEHAVIOUR OF *MELITTOBIA AUSTRALICA* GIRAULT,
1912, (HYMENOPTERA: EULOPHIDAE)

EDWARD DAHMS
Queensland Museum

ABSTRACT

The courtship behaviour of *M. australica* Girault, 1912 is discussed in detail and compared with that of *M. acasta* (Walker, 1839) and *M. chalybii* Ashmead, 1892.

Members of the genus *Melittobia*, where both sexes are known, show such extreme sexual dimorphism that the males and females of a species are not readily associated. *M. australica* Girault, 1912 shows typical dimorphism having a dark female, normal in form for a eulophid and pale brown males with abbreviated wings, modified antennae, and without compound eyes. The male's scape is greatly enlarged, pyriform in shape being expanded distally and bearing a ventral groove capped distally by a flap-like pedicel (Plate 28, A). During courtship the female's antennal club is clasped in this groove.

On emergence males remained close to the developing pupae and were observed to wander over the pupae palpating them with their antennae. The males were not observed to feed and never leave the host cell in which they emerged. If a male encountered another, a brief excited tussel ensued, but rarely was any injury inflicted. This contrasts with records of *M. acasta* (Walker, 1839) and *M. chalybii* Ashmead, 1892. Graham-Smith (1919) working with *acasta* noted that the males emerged first and there were fights in which the weaker were mutilated or killed. He recorded one fight as lasting for an hour and rarely did he find more than one male in a host puparium. Balfour-Browne (1922) noted that in *acasta* the incidence of such fights declined as the females began to emerge. Buckell (1928) recorded the males of *chalybii* as being extremely pugnacious and fighting fiercely until one was killed. Schmieder (1933), however, observed that no duels of this intensity in *chalybii* occurred even when a number of males were confined together in close quarters.

The males of *australica* searched for females with their short wings upright and their antennae outstretched. They were readily able to distinguish between males and females and in many cases when mated females were encountered the male did not attempt courtship. However, as the ratio of mated to unmated females increased the incidence of attempted courtship with females increased. This was perhaps a response to reduced encounters with unmated females. Under natural conditions this situation would not arise as the females disperse soon after mating. Where males attempted courtship with

mated females the latter did not submit passively, but attempted to walk off as the male mounted, or tucked their antennae beneath their heads out of reach. Where the males were able to proceed with courtship, attempts at copulation brought about no response from the females, and the males dismounted.

Unmated females were observed to solicit the attention of males. It was common to observe three or four females standing around a male engaged in courtship palpating him with their antennae. When approached by males, unmated females submit passively and courtship proceeds as follows. The male mounted the female's dorsum and used his antennae to orientate facing in the same direction as the female. His fore tarsi grasped the female around the cervix just behind the head, his mid tarsi were swung forwards and held out to either side of the female's head, his hind tarsi were braced against the female's abdomen or hind legs. The female's antennal club was fitted into the ventral groove of the male's scape, the male's wings were folded flat where they remained throughout courtship and copulation, and his abdomen was arched with its tip resting on the female's dorsal abdomen at about the second gastral segment.

Courtship was a long and involved procedure which lasted for up to 15 minutes. It may be discussed under two headings, antennal rubbing and kicking.

ANTENNAL RUBBING: Antennal rubbing alternated with kicking and involved the up and down squeezing motion of the flap-like pedicel. This resulted in oscillation of the female's club within the scape groove of the male's antenna and this oscillation was observed to alternate between the left and right antennae. Initially this was of short duration, 5–6 seconds, but gradually increased up to 19–21 seconds towards the end of the courtship period. During antennal rubbing the mid tarsi which were held either side of the female's head were noted to tremble.

KICKING: At the end of each antennal rubbing period the mid tarsi were swung above the female's head and then down to the level of the middle of her eyes in one relatively slow motion. At this stage there was a pause of 1–2 seconds after which the mid tarsi were swung down suddenly and rapidly accompanied by a kick of the male's hind legs braced against the female. The kick resulted in jerking of the whole body of the male. The mid tarsi returned to their position on either side of the female's head and antennal rubbing began again. Kicking was vigorous at the start of courtship, but diminished in intensity with time.

COPULATION: Immediately before copulation antennal rubbing ceased. There followed two or three convulsive movements of the male's body accompanied by the up and down motion of his mid tarsi. The male moved backwards maintaining his grip upon the female's antennae so that her head was pulled backwards until her frons was horizontal. At this stage the male released his grip upon the female's antennae and moved backwards passing the tip of his abdomen over and under that of the female. The female opened her genital aperture and copulation, lasting 8–10 seconds, took place. During copulation the female remained with her frons horizontal and the male had the distal

scape of his antennae braced against the dorsum of the female about half way along her wings (Plate 28, C).

In those cases where the male persisted in courtship with a mated female her head did not remain with the frons horizontal after release of her antennae and she did not open her genital aperture. Attempts at copulation by the male were unsuccessful.

The male antennal modifications of *acasta* and *chalybii* were recorded by various workers to be used during courtship in a similar fashion to those of *australica*. There are detailed descriptions of both species, (*acasta* — Parker and Thompson, 1928; *chalybii* — Hobbs and Kronic, 1971) which can be compared with *australica* and significant differences may be noted.

In *acasta* the body of the female was held by the male's fore and mid legs while the hind legs were used to stroke her lateral thorax. The hind legs stroke the thorax rhythmically beginning slowly and finishing with an abrupt jerk. At the same time, possibly alternating with the above, antennal rubbing occurs. After 4–5 minutes the behaviour of the male changed. The wings were beaten rapidly between strokes of the legs. The movements of the legs changed to a dorsoventral direction and the tarsi vigorously rubbed the sides of the female's thorax. Antennal rubbing deviated becoming more animated and then the convulsive jerks as in *australica* occurred just before copulation.

Hobbs and Kronic (1971) suggest that the mating habits of *chalybii* and *acasta* are similar. Comparing their observations on *chalybii* with those of Parker and Thompson (1928) on *acasta* it appears that this suggestion has some merit. However, there are a few discrepancies and it is felt that no definite decision could be made until standardised and more detailed observations on the two species are available.

Both differ in this behavioural aspect from *australica*. Such differences would presumably act as a reproductive isolating mechanism although it is a little difficult to find a reason for this necessity. *M. australica* is the sole species recorded from Australia whereas *acasta* and *chalybii* occur together in the Neotropics. Even so the males do not leave the host cell in which they emerge and the females are fertilised before they leave. Flanders (1943) adds another point of confusion by stating that within the genus *Melittobia* two different species may court and mate. Perhaps a much needed revision of the genus plus standardised and more detailed observations on the biology of the group may shed more light on the subject.

ACKNOWLEDGEMENT

The electron scan photograph of the male antenna (Plate 28A) was produced by the Electron Microscope Department, University of Queensland.

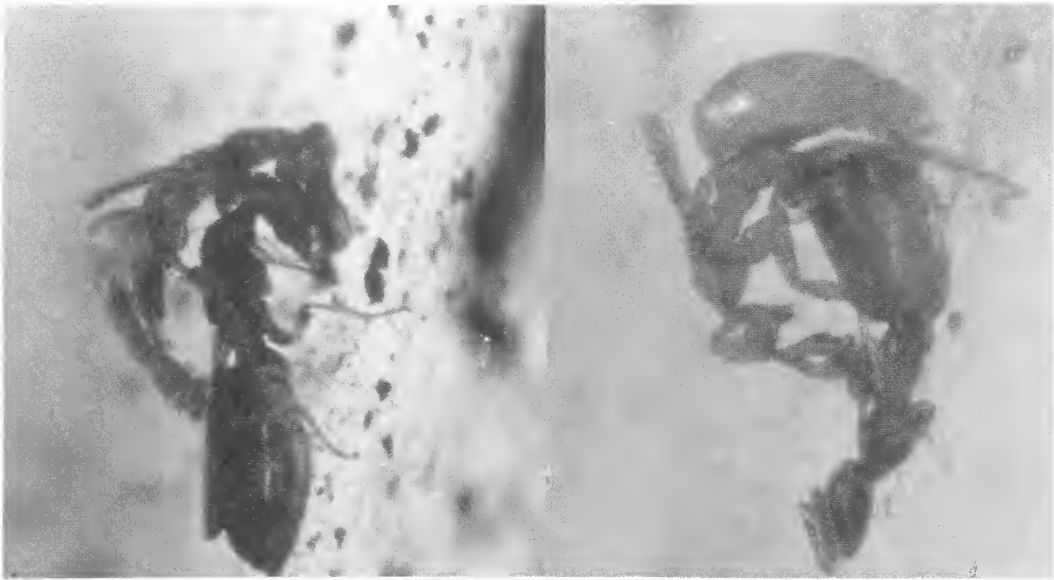
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PLATE 28

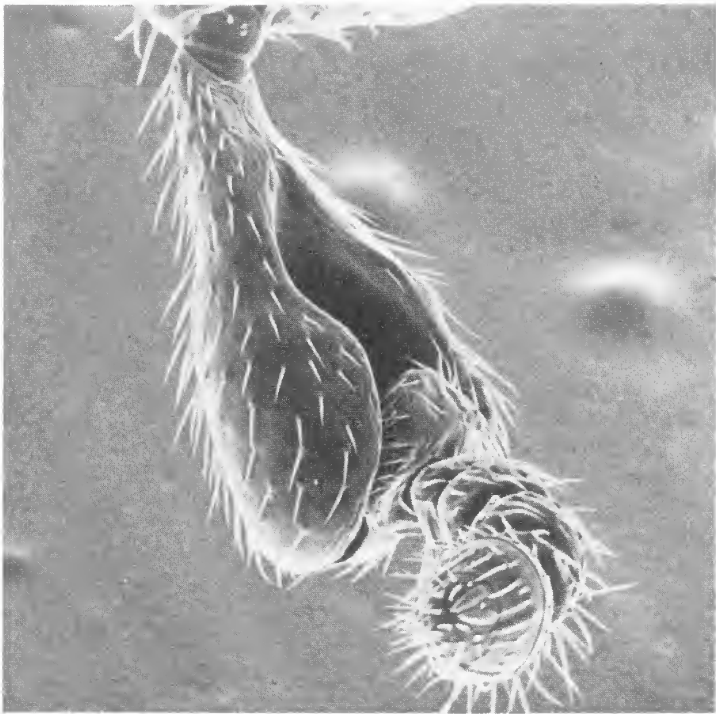
- A: Ventral view *Melittobia australica* male antenna.
- B: Courtship *M. australica*.
- C: Copulation *M. australica*.



B

C

A





STUDIES OF '*PORTUNUS GLADIATOR* COMPLEX' AND
RELATED SPECIES OF *PORTUNUS* (CRUSTACEA: DECAPODA).

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ABSTRACT

Confusion over *Portunus gladiator* Fabricius *P. gladiator*: Stephenson and Campbell, and *P. pseudoargentatus* Stephenson has been resolved. The species normally regarded as *P. gladiator* Fabricius becomes *P. haanii* (Stimpson); the species first named *Cancer gladiator* by Fabricius is synonymised with *P. sanguinolentus* (Herbst) and a neotype of *Cancer gladiator* has been deposited in the Queensland Museum. *P. pseudoargentatus* is a synonym of *P. haanii*, and *P. gladiator*: Stephenson and Campbell becomes *P. australiensis* sp. nov.

In 1959 Stephenson and Campbell identified two Australian portunids as *P. gladiator* Fabricius and gave a reasonably full description. In 1962 Crosnier, in reporting upon Madagascar portunids noted three main differences between material he identified as *P. gladiator* Fabricius and the descriptions of Stephenson and Campbell. While noting that these may have been due to size differences, he thought that two different species were involved. This was confirmed by Stephenson and Rees (1967a) who decided that a decision upon which of the two forms should be referred to Fabricius's species should await critical examination of Fabricius's material.

Through the kindness of Dr T. Wolff of the University Zoologiske Museum, Copenhagen, one of the original specimens upon which *P. gladiator* Fabricius, 1798 was based has been available for study, and photographs of a second specimen have been provided. It thus became clear that Crosnier's material belonged to Fabricius's species of 1798.

Meanwhile in 1961 Stephenson described a third species of the present 'complex'—*P. pseudoargentatus*. Crosnier (1962) in recording two Japanese specimens of this species in European museums, previously identified as *P. gladiator*, noted the probability of past confusions between *P. gladiator* and *P. pseudoargentatus*. It was clearly desirable to examine as many relevant specimens as possible, particularly because it became evident

that *P. gladiator* Fabricius varied in features which had been used in specific diagnoses. This necessitated biometric studies and these revealed that *P. pseudoargentatus* was a synonym of *P. gladiator* Fabricius, 1798.

A final point of confusion arises from the fact that Fabricius appears to have used the epithet *gladiator* on two occasions to refer to different species. The first use is in Fabricius (1793, p. 449) with reference to *Cancer gladiator*, and refers to specimens collected by Captain Cook in Australian waters—the details are ‘... in Nova Hollandia Mus. Dom. Banks’. We now have a considerable knowledge of the Australian portunid fauna (see for example Stephenson, 1972), and there have been only two recordings which could have been conspecific with *P. gladiator* Fabricius, 1798 in the last century. The first was by Haswell (1882) from Queensland waters. The specimens are no longer available and there is a possibility from the very general nature of Haswell’s description that the material was misidentified. The second records were Stephenson’s (1961) as *P. pseudoargentatus*. It would be unexpected for Captain Cook to have obtained, in his somewhat desultory collecting of portunids, a species which now appears to be anything but widespread in Australian waters.

Captain Cook’s specimens are not available, and a direct check of their identity can not be made. The only relevant comments upon the specimens are by Latreille (1825, p. 190) who synonymises them with *P. sanguinolentus* (Herbst, 1783). While it appears that Latreille may not have examined the material, we do know that *P. sanguinolentus* is common on sandy bottoms in the moderately shallow waters off the Queensland coast, and might well have been obtained by H.M.S. ‘Endeavour’. Since some finality is required, we have decided to accept Latreille’s synonymisation. As a result *P. gladiator* Fabricius, 1798 becomes a junior homonym of *P. gladiator* (Fabricius, 1793). We have selected a specimen of *P. sanguinolentus* (Herbst, 1783) as a neotype of *P. gladiator* (Fabricius, 1793), (Male, L = 65.8 mm, B = 149.7 mm, QM W3683, 6 miles N. of Skirmish Pt, S. end Bribie I., 4–6 fm, 17.v.1972) thereby eliminating this epithet. While this is to be regretted it appears to be the only course which avoids distortion of such facts as are known.

The full synonymy of *P. gladiator* Fabricius, 1798 is given later and from this it is evident that the first acceptable name is *Amphitrite haanii* Stimpson, 1858, based upon one of de Haan’s specimens of *Portunus* (*Amphitrite*) *gladiator*. Dr L. B. Holthius has kindly informed us that this specimen is existent in the Rijksmuseum, Leiden, and clearly this becomes the holotype.

Material for the present study has been borrowed from the institutions and individuals listed below, and we are deeply grateful to them: Australian Museum, (A.M.) per Dr D. J. G. Griffin; British Museum, (B.M.) per Dr R. W. Ingle; Office de la Recherche Scientifique et Technique Outre-Mer, Madagascar, per Dr A. Crosnier; Paris Museum, (P.M.) per Mme Danièle Guinot; Queensland Museum (Q.M.) per Mr B. M. Campbell; Strasbourg Museum, per Dr F. Gouin; United States National Museum, (U.S.N.M.) per Dr R. B. Manning; Univ. Zöologische Museum, Copenhagen, per Dr T. Wolff; Western Australian Museum, (W.A.M.) per Dr R. W. George. Appendix 1 lists details of all specimens within the ‘complex’ which were examined, while Appendix 2 lists borrowed material which had been identified as *P. gladiator* by various other workers, but which lies outside the ‘complex’.

The first objective in the work was to establish whether or not '*P. gladiator* Fabricius' and *P. pseudoargentatus* Stephenson were distinct, and is detailed in the next section. Following this the synonymy of '*P. gladiator* Fabricius' is detailed and discussed, and two species in the complex are then described—these are *Portunus haanii* (Stimpson) (= *P. gladiator* Fabricius, 1798) and *P. australiensis* (= *P. gladiator*: Stephenson and Campbell, 1959).

RELATIONSHIPS BETWEEN *P. HAANII* (STIMPSON) AND *P. PSEUDOARGENTATUS* STEPHENSON

The differences between *P. gladiator*: Stephenson and Campbell and the material studied in this section are sufficiently obvious to permit distinctions by means of the normal types of specific descriptions. This did not apply to the specimens in various collections which had previously been identified as *P. gladiator* Fabricius and as *P. pseudoargentatus* Stephenson. Stephenson and Rees (1967a, p. 25) summarised the differences between the two 'species' and stated for *P. pseudoargentatus*: 'b. Form of male abdomen. The ultimate segment relatively long and without concave lateral borders, penultimate segment not swollen in distal third. c. Relatively narrower fifth merus. In *P. pseudoargentatus* breadth is about 0.75 times length in *P. gladiator* about 0.9 times.'

Examination of the present collections showed that these and other features appeared to vary with specimen size and biometric studies were undertaken in all attributes which were readily quantified. The remaining possible differences are treated in a more classical way.

(A) BIOMETRICAL STUDIES

The following were measured:

- (1) Lengths and breadths of carapaces, using dial calipers, with results given to nearest 0.5 mm. Length was from the tips of the median frontal teeth to the mid-point of the posterior edge of the carapace. Breadth was between the tips of the last anterolateral teeth. In cases where these tips were damaged, an estimate was made to the nearest 1 mm of probable breadth before damage. From the above data length/breadth (l./b.) ratios of carapaces were derived. Because damage affected breadth, carapace lengths were used to determine whether ratios were size-dependent.
- (2) Lengths and breadths of the merus of the fifth legs were measured in arbitrary units (gradations of eyepiece micrometer). Length/breadth ratios gave values approximating to 1.00 and are accurate to about 0.02.
- (3) The relative concavity of penultimate segment of the male abdomen was measured as the difference between the maximum breadth of this segment (which is usually about $\frac{2}{3}$ of the length from the distal border) and the minimal breadth (about $\frac{1}{3}$ this length), divided by the minimal breadth. These values range from ca. 0.4 to zero and are accurate to about ± 0.005 .

- (4) Lengths of the penultimate segment were measured in the mid line, and the ratio length/maximum breadth was used as a measure of overall shape. Values approximate to unity and are accurate to about 0.02.
- (5) In a similar way the length/breadth ratio of the ultimate segment was derived again to about 0.02.
- (6) From the above data the ratio of the lengths of ultimate to length of penultimate segments were obtained, with accuracy again ca. 0.02.

Of the six ratios obtained above, one appeared to be completely independent of specimen size; this was l./b. carapace. Means (\bar{X}) and standard deviations (s) were obtained and data for '*P. gladiator* Fabr.' are (\bar{X} 0.557, s 0.020, n 55) and for *P. pseudoargentatus* are (\bar{X} 0.565, s 0.050, n 8). Clearly there is no significant difference.

Further analyses showed there was no significant difference between males of '*P. gladiator* Fabr.' (\bar{X} 0.555, s 0.017, n 32) and females (\bar{X} 0.559, s 0.020, n 23).

Other ratios in which there were possibilities of a size factor are given as scatter diagrams. These are l./b. ultimate segment male abdomen (Fig. 1), l./max.b. penultimate segment (Fig. 2), and l. ultimate/ l. penultimate segment (Fig. 3). The first of these shows that the two 'species' overlap extensively in their ratios, with one specimen (29 mm) of *P. pseudoargentatus* lower than and separated from the remainder. The second is similar, with in this case a different specimen of *P. pseudoargentatus* higher than and separated from the remainder. The third again shows overlap, with the 29 mm specimen and the 35 mm holotype of *P. pseudoargentatus* lower than the remainder. Clearly if all specimens labelled as *P. pseudoargentatus* have been correctly identified, this species cannot be separated from '*P. gladiator* Fabr.' It should be noted that the holotype of *P. pseudoargentatus* is at the extreme of the range as regards the ratio l. ultimate/l. penultimate segment of male abdomen.

The two remaining ratios show clear indications of dependence upon specimen size (see Figs. 4 and 5). Easy conversions of data (e.g. logarithmic) failed to produce straight line regressions, so data are considered on the bases of the scatter diagrams.

FIG. 1: Length/breadth of ultimate segment of male abdomen against carapace length in mm. Each symbol represents one specimen with ● originally identified as *P. gladiator* Fabricius; ■ originally identified as *P. pseudoargentatus* Stephenson; and ★ juvenile specimen.

FIG. 2: Length/maximum breadth of penultimate segment of male abdomen against carapace length in mm. Symbols as in Fig. 1, each symbol represents one specimen.

FIG. 3: Length of ultimate segment of male abdomen/length of penultimate segment against carapace length in mm. Symbols as in Fig. 1, each symbol represents one specimen.

FIG. 4: Maximum breadth minus minimum breadth/minimum breadth of penultimate segment of male abdomen against carapace length in mm. Symbols as in Fig. 1, each symbol representing one specimen.

FIG. 5: Length/breadth of merus of fifth leg against carapace length in mm. Symbols as in Fig. 1, each symbol represents one merus, in most cases two per specimen.

FIG 1

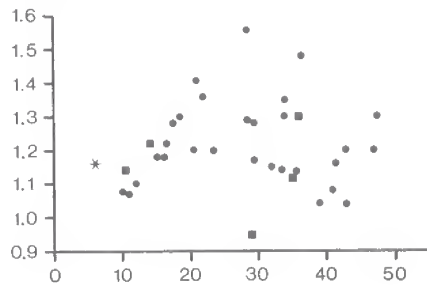


FIG 2

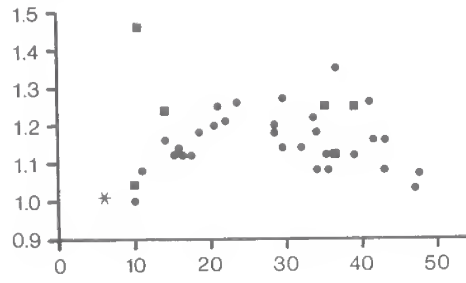


FIG 3

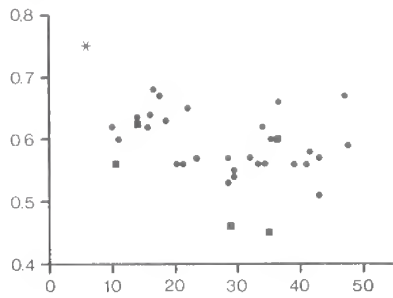


FIG 4

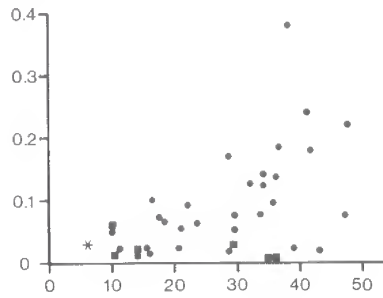


FIG 5

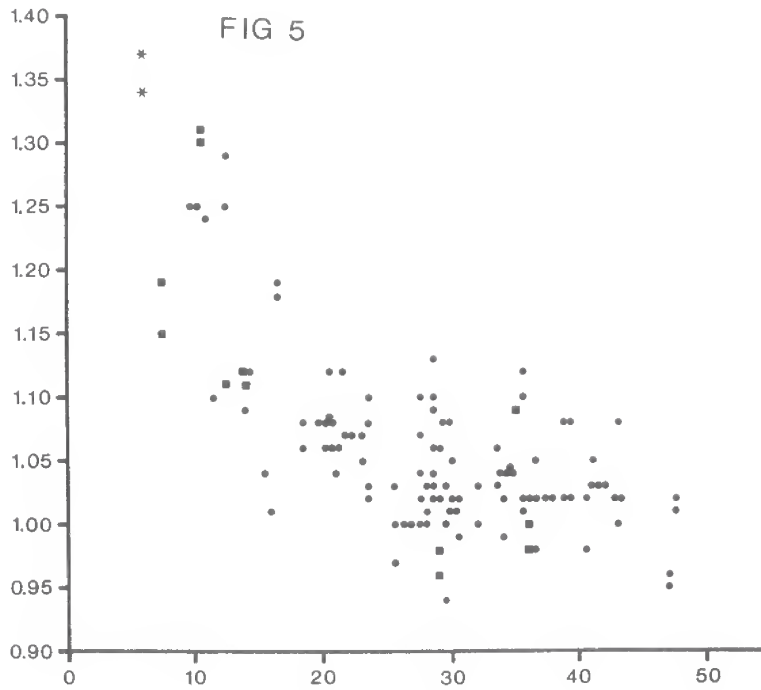


Figure 5 shows that the l./b. ratio of the fifth merus decreases with increasing size of specimen. The 35 mm holotype of *P. pseudoargentatus* lies within the range shown by '*P. gladiator*' material. A 6 mm specimen which we had considered to belong to *P. pseudoargentatus* partly on the basis of a high ratio, apparently owes this to its small size. Figure 4 indicates the concavity of the penultimate segment of the male abdomen in terms of the ratio max. b. — min. b./min. b. All six specimens identified as *P. pseudoargentatus* give low ratios, and once again the holotype has the most extreme value. Because of overlap in values, concavity of this segment would not appear to have diagnostic value.

In summary, biometric study appears to show a complete gradation between specimens identified as *P. gladiator* Fabr. and *P. pseudoargentatus* respectively. In three of the six data sets, the holotype of *P. pseudoargentatus* is at or close to the extreme of the extensive ranges.

(B) MALE FIRST PLEOPODS (Figs. 6A–I, 8A–I, 9A–I)

Only a few species of the genus *Portunus* have pleopods sufficiently unique to give easy diagnosis—examples are *P. granulatus* (H. Milne Edwards) and *P. dubius* (Laurie). In the remainder the general shape and the nature of the subterminal armature are of value, but require detailed descriptions and figures. In some cases pleopod structure varies within a species and in *P. argentatus* (A. Milne Edwards), Stephenson and Rees (1967a) showed that there were two 'forms' differing only in male first pleopods and abdomens. In *P. rugosus* (A. Milne Edwards) the above authors again showed that two 'forms' existed, separated by the male first pleopods and other structures. Variation in pleopod structure in further species of *Portunus* is less well documented, but Stephenson (1968) has noted that this does occur in specimens of *P. pelagicus* from widely separated areas. With this knowledge of the potential variability of male first pleopods in certain *Portunus* spp., their structures in the present complex were investigated in detail in the available specimens of '*P. gladiator* Fabr.' and *P. pseudoargentatus*.

Figures and descriptions of the pleopods of *P. gladiator* Fabricius and *P. pseudoargentatus* Stephenson are given by Crosnier (1962, figs. 82–3, p. 52) and by Stephenson (1961, figs. 2A, 3F, p. 110) respectively, and Crosnier (p. 148) gives additional comments. The following features have been used for separation:

- (1) greater curvature near the middle of *P. pseudoargentatus*, Crosnier (p. 52) states of *P. gladiator* '.... recourbé à angle droit vers son milieu ...', and of *P. pseudoargentatus* '... plus recourbé en son milieu ...'. Actually Crosnier's figure of *P. gladiator* (fig. 78) shows an angle a little greater than 90°, and not sensibly different from Stephenson's figure of *P. pseudoargentatus* (fig. 2A).
- (2) broader tip in *P. pseudoargentatus* (fide Crosnier). This is apparent in the figures quoted above.

In addition Stephenson's figures of the armature of the top of the pleopod in *P. pseudoargentatus* (Fig. 3F) shows a much denser pattern of spinules than Crosnier shows in *P. gladiator* (figs. 82–3).

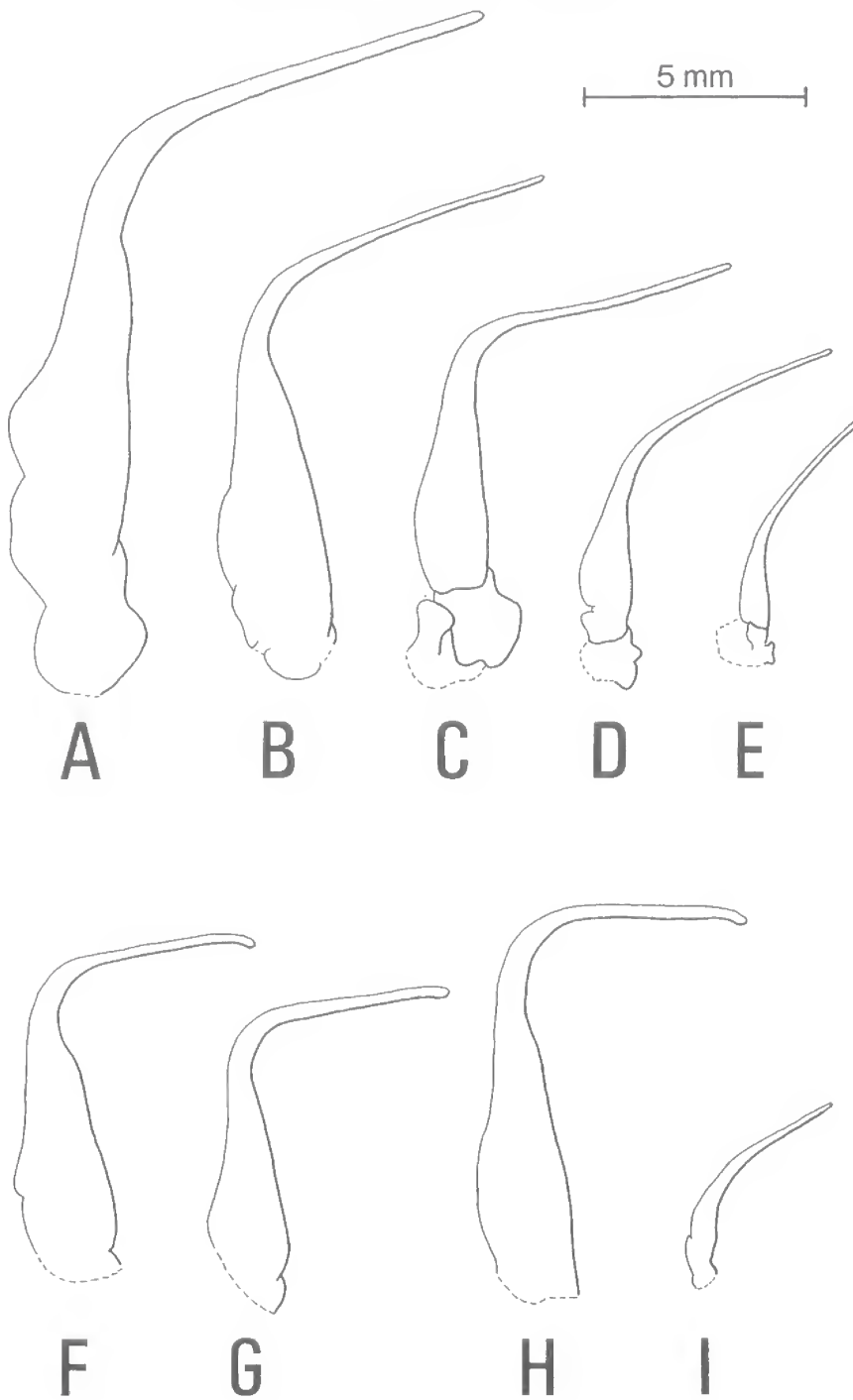


FIG. 6: Male first pleopods. A-E, *P. haanii* showing 'normal' increase in curvature with increase in carapace breadth; F-H, *P. haanii* 'unusual' specimens. I, *P. australiensis* holotype. (Details of specimens are preceded with bold capitals in Appendix 1.)

Pleopods of the present specimens (where examinable) mostly belonged to a graded series, related to the size of the specimens. The general form of the pleopod in members of this series is shown in Figs. 6A–E. Three specimens did not exactly agree with this series. Compared with pleopods of the same general size they had greater curvature near their centres, and had stouter tips. These are shown in Figs. 6F, G, H; F and G being from the (only) two specimens in one collection. H is from the holotype of *P. pseudoargentatus*.

The two diagnostic features of *P. pseudoargentatus* are confirmed for the holotype, but are equally exhibited by two specimens which in all other particulars appear to be typical *P. gladiator* Fabricius.

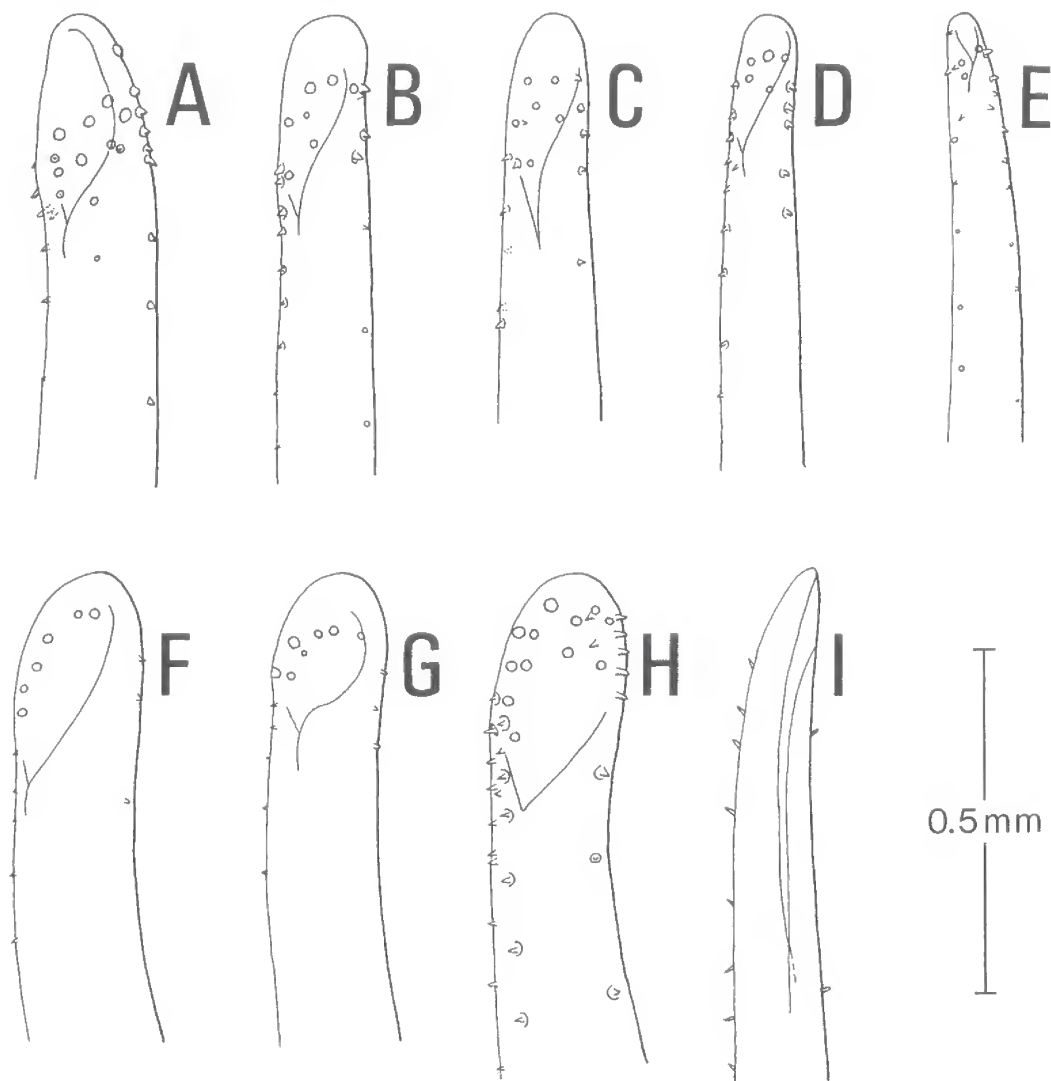


FIG. 7: Upper surface of tips of male first pleopods. Specimens as in Fig. 6.

Tips of pleopods of the above specimens are shown in Figs. 7A–H, 8A–H. These confirm the relative robustness of the tips of specimens F, G and H and show considerable variation in the subterminal armature. Difficulties were encountered in elucidating the details of this spinulation, particularly in the thin terminal area beyond the aperture of the appendage. Here each spinule arises from a roughly circular area, more transparent than its surroundings, and these areas are more clearly visible in a ventral view of the appendage. However, in those cases where spinules could be recognised these are directed dorsally.

Common features in all pleopods were relative absence of spinules from upper and under surfaces (excepting in their terminal area), lines of spinules on or near both inner and outer sides, and a band of spinules near the tip directed into the flaring portion of the aperture.

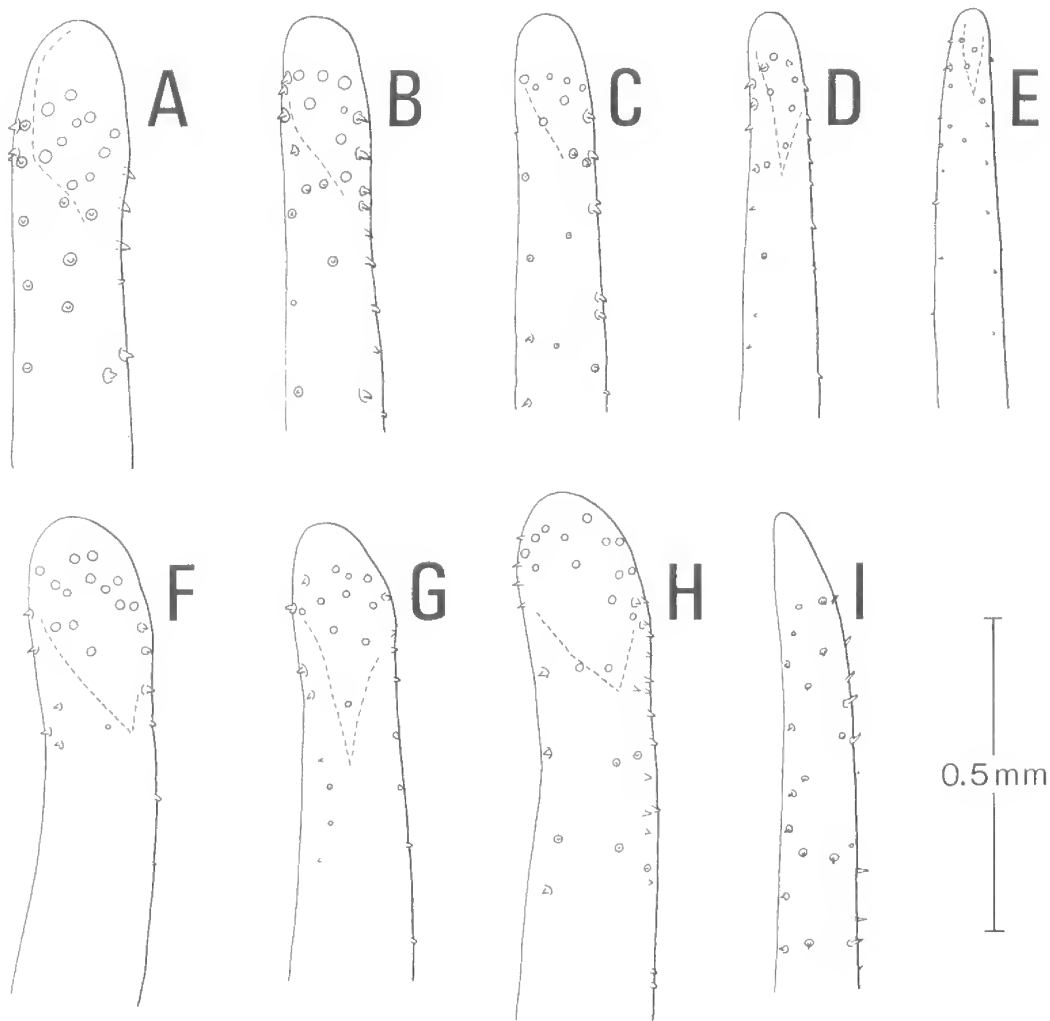


FIG. 8: Lower surface of tips of male first pleopods. Specimens as in Fig. 6.

In the series A–E with increasing size of appendage, the spinules become larger and more numerous, with subterminal concentrations on inner and outer sides. In F and G the spinules are relatively small for the size of the appendage, are sparsely distributed on inner and outer sides, and are without the subterminal concentrations. In H the spinules are smaller but are more numerous than from appendages of the same size in the A–E series. The upper surface bears a row of spinules near its outer margin which is not or is scarcely recognisable on the remainder. Figs. 7F, 8F, 7G, 8G, 7H and 8H show a further difference from the remainder of those figures in having the spinules of the thin terminal area extending closer to the tip. This distinction was not absolute; two other specimens otherwise resembling 8B, 9B showed this feature.

Overall it is concluded that all pleopods examined are variants of a single specific pattern. This conclusion has already been indicated in two papers recently published (Stephenson, 1972a, b).

(C) CARAPACE GRANULATION AND PIGMENTATION (Figs. 9A, B)

Stephenson and Rees (1967a, p. 25) stated that *P. pseudoargentatus* differs from Crosnier's specimens of *P. gladiator* Fabr. in having: 'A more strongly embossed carapace with coarser granulation. In particular the cardiac, lateral postcardiacs, posterolaterals,



FIG. 9: Carapace granulation. A, *P. haanii* male, Fort-Dauphin, Côte sud de Madagascar, coll. A. Crosnier ex. P.M.; B, *P. haanii* male, Shimizu, Suruga, Japan, U.S.N.M. 112423; C, *P. australiensis*, holotype, A.M. P12602.

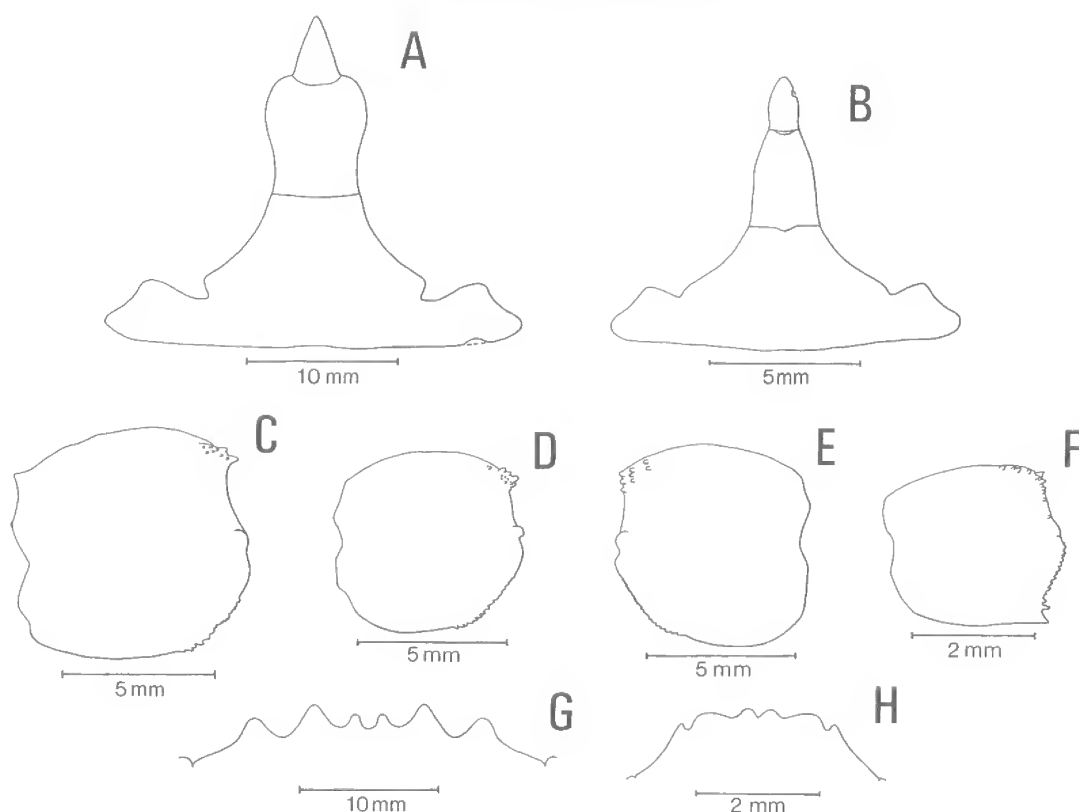


FIG. 10: A, Typical male abdomen *P. haanii* (A.M. W2688); B, Male abdomen *P. australiensis* (A.M. P12602); C, Right merus *P. haanii* (Q.M. W2688); D, Right merus *P. haanii* (U.S.N.M. 72540–54 mm specimen); E, Left merus *P. haanii* (Galathea sta. 346); F, Right merus *P. australiensis* (A.M. P12602); G, Typical carapace front *P. haanii* (Q.M. W2688); H, Front of juvenile *P. haanii* (U.S.N.M. 39801).

and two mesobranchials are larger and less diffuse than in *P. gladiator*.⁷ Examination of the present material showed that there was gradation between strongly embossed carapaces with coarser granulation (which tended to occur in smaller specimens) and less strongly embossed more finely granular carapaces. Figs. 9A, B show the extremes of variation and approximately the average conditions. The variation is expressed verbally in the specific description.

Pigmentation of the holotype of *P. pseudoargentatus*, after two months in alcohol was described by Stephenson (1961). This differs from that of the pigmented specimens of *P. gladiator* Fabricius (as described below) only in the presence of a conspicuous purplish red mark on the propodus of the fifth leg—only the left leg was present. After almost 12 years of alcohol preservation this mark is the only remaining pigmentation and is now pink and presumably on prolonged preservation it will disappear. Apart from the holotype, none of the specimens identified as *P. pseudoargentatus* had any significant pigmentation after preservation.

(D) CONCLUSION

When all specimens previously identified as *P. pseudoargentatus* are compared with those of '*P. gladiator* Fabr.' there is considerable overlap. This is due to the great variability of features which had been used in diagnosis. In a few features the holotype of *P. pseudoargentatus* is at the extreme of a range of variation and while there is not a sufficient gap between this specimen and the remainder to merit retention of specific status, there is a parallel between its morphological status and biogeographic isolation—it is the only existent specimen from Australian waters. If further Australian specimens are obtained and agree closely with the holotype of *P. pseudoargentatus* the possibilities of clines or subspecies of *P. haanii* Stimpson (= *P. gladiator* Fabricius, 1798) will merit investigation.

SYNONYMY OF *P. HAANII*

- Portunus gladiator* Fabricius, 1798, p. 368. Latreille, 1825, p. 189. Rathbun, 1902, p. 26. Crosnier, 1962, pp. 51–5, 148, 150, figs. 72, 76, 78, 82–3, pl. 3, fig. 2. Sakai, 1965, p. 118, col. pl. 57, fig. 1 (record only). Stephenson and Rees, 1967, pp. 24–5; 1968, p. 293. Stephenson, 1972a, pp. 16, 39; 1972b, p. 135 (record only).
- Portunus (Amphitrite) gladiator* Fabricius; de Haan, 1850, p. 39, pl. 1, fig. 5.
- Amphitrite Haanii* Stimpson, 1858, pp. 38–9; 1907, p. 79.
- Neptunus gladiator* Fabricius: A. Milne-Edwards, 1861, p. 330. Richters, 1880, p. 152 (record only). Müller, 1886, p. 475 (record only). de Man, 1887, pp. 69–70. Henderson, 1893, p. 367 (record only). Sakai, 1934, p. 303 (record only).
- Neptunus (Amphitrite) gladiator* Fabricius: Miers, 1886, p. 177. Ortmann, 1893, p. 73. Alcock, 1899, pp. 35–6. Laurie, 1906, p. 412. Parisi, 1916, p. 173 (record only). Balss, 1922, p. 107. Shen, 1937, pp. 101–3, fig. 2. Sakai, 1939, pp. 390–1, fig. 5, col. pl. 47, fig. 3.
- Portunus (Achelous) gladiator* Fabricius: Rathbun, 1910, p. 36 (record only).
- Callinectes gladiator* Fabricius: Stebbing, 1915, p. 58 (record only).
- Monomia gladiator* Fabricius: Barnard, 1950, p. 156. Fourmanoir, 1954, p. 9 (record only).
- Portunus pseudoargentatus* Stephenson, 1961, pp. 109–11, figs. 2A, 3F, pl. 2, fig. 4, pls. 4F, 5D; 1972a, pp. 16, 41–2; 1972b, p. 137. Crosnier, 1962, pp. 148, 150 (under *P. gladiator*). Stephenson and Rees, 1967, p. 25; 1968, pp. 294–5.
- [Not] *Cancer gladiator* Fabricius, 1793, p. 449 (= juv. *P. sanguinolentus* (Herbst), fide Latreille, 1825, p. 190).
- [Not] *Cancer Menestho* Herbst, 1803, p. 34, pl. 55, fig. 3.
- [Not] *Lupea gladiator*: H. Milne Edwards, 1834, p. 456.
- [Not] *Portunus (Amphitrite) gladiator*: de Haan, 1850, p. 65 pl. 18, fig. 1 (= *P. orbitosinus* Rathbun, 1911).
- [Not] *Amphitrite media* Stimpson 1858, p. 39; 1907, pp. 79–80, pl. 10, fig. 1 (= ?*P. orbitosinus* Rathbun, 1911).
- [Not] *Callinectes tumidus* Ordway var. *gladiator* Benedict, 1893, p. 537, fide Barnard, 1950, p. 156.
- [Not] *Portunus gladiator*: Stephenson and Campbell, 1959, pp. 110–1, figs. 2J, 3J, pl. 3, fig. 2, pls. 4I, 5J (not 4J as stated) (= *P. australiensis* sp. nov. (see later)).
- [?] *Amphitrite gladiator* (Fabricius): Haswell, 1882, p. 84.

As indicated in the introduction the first use of the epithet *gladiator* is in Fabricius (1793, p. 449) with reference to *Cancer gladiator*, which Latreille (1825, p. 190) in company with Fabricius's *C. defensor*, lists as a synonym of *P. sanguinolentus* (Herbst).

Fabricius's above description of *C. gladiator* is so generalised that it could apply to many species. It almost certainly does not apply to the species he called *Portunus gladiator* in 1798 (p. 368) (and which has become accepted as *the P. gladiator*). Further evidence is that the habitat of *C. gladiator* is stated as 'in Nova Hollandia Mus. Dom. Banks'. As indicated, *P. gladiator* appears to occur quite rarely in Nova Hollandia (= Australia). It is clear that whether or not we accept Latreille's synonymisation of *Cancer gladiator* Fabricius; 1793, under *P. sanguinolentus* (Herbst, 1783):

- (a) *C. gladiator* Fabricius, 1793, is in the same genus as his *P. gladiator*;
- (b) the two are different species;
- (c) following the first use of the epithet *gladiator* the second use is as a junior homonym; and
- (d) hence under the International Rules the name should be replaced.

The next possible name is *Cancer menestho* Herbst, 1803, which Latreille (p. 189) gives as a queried synonym of Fabricius's *P. gladiator*. Later workers have omitted the query without justifying so doing. Herbst's figure (fig. 3) shows a *Portunus* with the posterior border of the arms of the chelipeds showing one distinct and protruding spine and a second non-protruding spine. Herbst's text states (pp. 35–6): 'Am innern Rande des Armes steht eine Reihe von vier nach vorne sich hinneigender Dornen, die nach oben zu werden etwas grösser; am Aussenrande steht ganz oben ein gleicher Dorn; bey grossen Exemplaren steht etwas hinter diesem noch ein zweiter von gleicher Grösse, bey den kleiner ist dasebst nur eine stumpfe Ecke. . . .'. All the present specimens including the smallest of *P. haanii* have two distinct spines on the posterior border of the arm, and on this basis Herbst's species is not a synonym. It might be *P. rubromarginatus* (Lanchester) but this has only a single spine on the posterior border of the arm and has a characteristic pigmentation which differs from that of *Cancer menestho*. Unless and until the range of Herbst's specimens can be re-examined their status must remain uncertain.

The first available specific epithet is *haanii*, used by Stimpson (1858, p. 38), but meanwhile in the chronology of the synonymy Latreille (1825, p. 189) is interesting. Referring to segments of the (male) abdomen he states: ' . . . l'avant-dernier un peu dilaté et arrondi latéralement à son extrémité.' He clearly refers to a '*P. pseudoargentatus*' form of abdomen.

H. Milne Edwards's (1834, p. 456) description of *Lupea gladiator* has been accepted into the synonymy by all later workers with the exception of Stimpson (1858, p. 38; 1907 p. 79) who noted that H. Milne Edwards's description of the carapace as 'peu ou point granuleuse' did not apply to de Haan's *Portunus (Amphitrite) gladiator* (see below). Stimpson evidently accepted that Milne Edwards's *L. gladiator* was Fabricius's *P. gladiator* and proposed the new name *Amphitrite Haanii* for de Haan's form. In fact de Haan's species is the same as Fabricius's (but see below), and the 'different' species, whose synonymy is uncertain appears to be Milne Edwards's. Further evidence for this is that Milne Edwards describes the front as 'très-relevé' which it is not.

De Haan (1850) gave a good figure of the present species (pl. 1, fig. 5) but a second figure (pl. 18, fig. 1) supposedly of this species is *P. orbitosinus* Rathbun.

Stimpson (1858) introduced two names, *Amphitrite Haanii* (p. 38) already commented on, and *A. media* (p. 39). The latter, which has not been figured, differs from the former in

having a shorter last anterolateral tooth, and the lateral and median frontal teeth of similar size. A. Milne Edwards (1861, p. 331) under *Neptunus medius* thought it was insufficiently precise to distinguish it from *P. gladiator* Fabricius, and this opinion was repeated by Ortmann (1893, p. 73). Alcock (1899, p. 35) accepted *A. media* as a queried synonym of *P. gladiator* Fabricius but it seems clear that it is not a synonym because of the noticeable difference in frontal teeth. Rathbun (1910) accepted this, but not Parisi (1916). It is unfortunate that Stimpson's type is not extant, because *A. media* greatly resembles *P. orbitosinus* Rathbun, and if they are identical, the former name would have priority.

Much of the synonymy is concerned with generic and subgeneric names, whose history need not be detailed; it has been outlined by Rathbun (1930, p. 33). A decision by the International Commission on Zoological Nomenclature (1956) has established the generic name as *Portunus*, and Stephenson and Campbell (1959) and Stephenson, Williams and Lance (1968) have concluded that there are no acceptable sub-generic divisions.

The most recent synonymy confusion owes much to the present senior author. The specimens which Stephenson and Campbell (1959) referred to *P. gladiator* belong to a different species, while, as shown earlier *P. pseudoargentatus* belongs to the present species.

DESCRIPTIONS OF SPECIES

P. haanii Stimpson (= *P. gladiator* Fabricius, 1798) is redescribed taking cognisance of its variability, and to include *P. pseudoargentatus*. The material identified as *P. gladiator* Fabricius by Stephenson and Campbell (1959) is renamed *P. australiensis* sp. nov. and also redescribed to clarify and amplify its distinctiveness from *P. haanii*. To avoid repetition, features common to the two species are listed first and not repeated. The species (with synonymy of one) are then described, with the full lists of specimens examined being listed in Appendix 1.

FEATURES COMMON TO BOTH SPECIES

FRONT: Four-lobed, laterals at least width of medians. Lower border of orbit with distinct tooth close to basal antennal joint.

ANTEROLATERAL TEETH: First stout and blunt, ninth a long spine directed outwards, second to eighth of progressively increasing length.

CARAPACE: Moderately broad (breadth ca. 1.8 times length). Anterolateral borders forming broad curve whose centre lies at or behind cardiac region. Postlateral junctions rounded and with right-angled projection on lower plane. Surface covered with widely spaced granulated areas separated by regions of dense pubescence. Granulated patches are: protogastrics, diffuse; mesogastrics; central gastric; metagastrics with distinct anterior termination; 2 cardials and 3 postcardials; anterolaterals; epibranchial; either 3 or 4 mesobranchials; 2 lateral postcardials and postlaterals; metagastrics forming broad transverse band with distinct almost ridge-like anterior termination.

CHELIPEDS: Stout, pubescent. Posterodistal border of arm bearing 2 sharp spines, anterior border with 4 spines. Wrist with 2 usual spines. Three usual carinae on upper surface of hand of which only innermost ends in a spine. Outer surface of hand with very distinct carina. Under surface of hand of cheliped typically bearing squamiform granules.

THIRD MAXILLIPED: Anteroexternal angle of merus strongly produced in lateral direction.

FIFTH LEG: Merus relatively long; $l/b = 0.96-1.10$.

***Portunus haanii* (Stimpson, 1858)**

(Figs. 6A-H, 7A-H, 8A-H, 9A-B, 10A, C-E, G-H)

DESCRIPTION

FRONT: Laterals rounded, or acute or right-angled, ca. three times width of medians, these usually rounded, sometimes acute. Upper border or orbit with distinct and prominent tooth (less distinct in small specimens). In smaller specimens indentation of front becomes shallower so that teeth appear relatively broader and front as a whole becomes increasingly sinuous.

ANTEROLATERAL TEETH: Second to eighth sharp although rounded in larger or worn specimens.

CARAPACE: In large specimens granulated area a relatively small proportion of total carapace area, in smaller specimens a relatively greater proportion granulated but still distinctly less than in *P. australiensis*. Frontal granular patches present; orbitals inconspicuous or absent. Postfrontals either absent or represented by patch of 2 to 8 granules. Protogastrics forming broad diffuse arc. Central gastric broad and diffuse with about 3 to 4 irregular rows of granules. Each mesogastric consisting of two widely separated ovoid patches. Two cardiacs well separated. Median postcardiacs small. Lateral postcardiacs relatively small. Anterolaterals consisting of relatively narrow and diffuse patches opposite second to fourth and fifth to sixth teeth, sometimes a few granules on bases of seventh and eighth teeth. Epibranchials almost forming curved ridges bearing a few scattered granules anterior to them. Four distinct and well separated mesobranchials. Postlaterals small and distinct

CHELIPEDS: Inner carina of upper surface of palm with relatively large subterminal spine. Outer surface of palm beneath pile of hairs not or faintly squamiform. In large males on inner surface of palm of cheliped a conspicuously granular central carina, with scattered granules lying on either side of it. In smaller males and in females central carina ill-developed and tending to squamiform. Inner sides of fingers strongly carinate and in large males, granular.

FIFTH LEG: Merus with anterodistal extremity typically with conspicuous projection consisting of numerous rounded or spiniform granules. In some relatively small specimens projection not conspicuous and merely a coarsely granular area. Posterodistal

border with regularly arranged granules (rounded or sharp) giving serrated appearance but without conspicuous projection.

MALE ABDOMEN: Somewhat variable in shape with penultimate segment in larger specimens distinctly swollen in distal third but not swollen in smaller specimens. Ultimate segment in larger specimens with concave lateral borders, in smaller specimens with convex borders. Ultimate segment ca. half length of penultimate (0.44–0.61 times). Ultimate segment slightly longer than broad (1.07–1.36 times). Penultimate segment also slightly longer than broad (1.06–1.43 times).

COLOUR: After prolonged alcohol preservation patches of pink pigment on proximal ends of spines of anterior border of arm, bases of inner wrist spines, two patches on inner carina on upper surface of palm, mottled patching on upper and outer surfaces of movable finger, also in groove between outer frontal tooth and inner supraorbital border and between inner and outer frontal teeth. In specimens kept for shorter period in alcohol e.g. seven years, additional areas of pink pigmentation are: posterior margin of carapace, postlateral granules, patches on upper surface of hand of cheliped and in one case on most carapace granules.

***Portunus australiensis* sp. nov.**

(Figs. 6I, 7I, 8I, 9C, 10B, F.)

Portunus gladiator: Stephenson and Campbell, 1959, pp. 110–I, figs. 2J, 3J, pl. 3, fig. 2, pls. 4I, 5J (not 4J as stated). Stephenson and Rees, 1967a, p. 24.

[Not] *Portunus gladiator* Fabricius, 1798, p. 368.

MATERIAL EXAMINED

HOLOTYPE: ♂ (28 mm), Ninety-Mile Beach between Cape Jaubert and Wallal, dredged 5 fm, Sept. 1929, A.M. P12602.

ALLOTYPE: ♀ (44 mm), dredged between C. Bossut and Broome, 5 fm, 11.x.1929, A.M. P12596.

DESCRIPTION

FRONT: Laterals ca. right-angled, about twice width of medians which are acute or rounded. Upper border of orbit without distinct and prominent tooth.

ANTEROLATERAL TEETH: Second to fourth blunt or right-angled, fifth to eighth sharp.

CARAPACE: Frontals and orbitals obvious in male but not in female specimen. Postfrontals represented by line of 3 or 4 granules. Protogastrics almost subdivided into 2, posterior portion merging with mesogastrics almost to form a granulated ridge. Central gastric narrow, anterior to mesogastric about 2 irregular rows of granules, posteriorly a single row. Mesogastrics forming transverse band with distinct anterior termination. Two cardiacs almost confluent. Median postcardiacs broad diffuse patch running almost to posterior border of carapace. Lateral postcardiacs relatively large. Anterolaterals consisting of relatively broad and dense patches of granules opposite second to fourth,

fifth to sixth and seventh to eighth teeth. Epibranchials forming almost straight ridges of granules with numerous scattered granules anterior to them. Two distinct anterior mesobranchials, posterior mesobranchial granulated areas merging into posterior laterals.

CHELIPEDS: Inner carina of upper surface of palm with relatively small terminal spine. Outer surface of palm with distinctly squamiform granules. Inner surface of palm of cheliped with central carina, of squamiform granules, with squamiform areas lying above it. Inner sides of fingers weakly carinate and not obviously granular.

FIFTH LEG: Merus with anterodistal extremity with inconspicuous cluster of spiniform granules. Posterodistal border serrated and with one or two distinct spines marking the edge of the border.

MALE ABDOMEN: Penultimate segment markedly converging in distal third, ultimate segment with convex lateral borders. Penultimate segment longer than broad (1.20 times). Ultimate segment much longer than broad (1.35 times), ca. half length of penultimate (0.56 times).

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APPENDIX I

MATERIAL EXAMINED OF *P. haanii* STIMPSON.

Illustrated specimens indicated by bold capitals.

Australian Museum: One ♀ (47 mm), P7680. One ♂ (62 mm), P7681, Ceylon, Pearl Banks Inspection, Moderagam Paar, 26.xi.1921; exchange Colombo Museum, Ceylon, Jan. 1925. One ♀ (44 mm), P14193, Troubadour Reef, approx. 10°S. 129°E., edge of Sahul Shelf, off Darwin, N.T., caught with dip net at surface over 17 fms 20.30 hrs, 6.ix.1949, coll. G. P. Whitley, 'Stanley Fowler' C.S.I.R.O. Exped.

British Museum: Four ♀ (37–57 mm), BM315–318, Madras, 15.vii.1892, coll. Henderson. One ♂ (74 mm), BM289, off Negambo, Gulf of Manaar, Ceylon, 22.v.1907, coll. Herdman. E One ♂ (28 mm), BM118, off Kaltura, 16.i.1934, coll. Herdman. Three ♂ (25–39 mm); one ♀ ovig (37 mm), BM116–117, Ceylon, Pearl Banks, Gulf of Manaar, 16.i.1934, coll. Herdman.

Office de la Recherche Scientifique et Technique Outre-Mer, Madagascar: One ♂ (84 mm), Fort-Dauphin, Côte sud de Madagascar, dans une nasse à langoustes, 20 m, coll. A. Crosnier. One ♀ (71 mm), Cap St André, Côte nord-ouest de Madagascar, chalutage 20 m sable vaseux, Juillet 1959, coll. A. Crosnier.

Paris Museum: One ♂ (52.5 mm), det. Crosnier 1962 *P. pseudoargentatus* Stephenson. One ♂ (66.5 mm), Sumatra, coll. M. Martin. A One ♂ (82 mm), Fort-Dauphin, Côte sud Madagascar, dans nasse à langoustes, Mai 1961, 20 m, coll. A. Crosnier.

Queensland Museum: B One ♂ (66 mm), W2688, NW Madagascar (from Dr A. Crosnier).

Strasbourg Museum: One ♂ (27 mm), dry, Kagoshima, Japan, 1882, coll. L. Döderlein. One ♂ (64.5 mm), Kochi, Japan, 1882, coll. L. Döderlein. (Previously identified as *P. pseudoargentatus* Stephenson, see Crosnier, 1962). Two ♂ (52 mm, other damaged); one ♀ (62 mm), Kochi, Japan, 1882, coll. L. Döderlein.

United States National Museum: One ♂ (70 mm); one ♀ (66 mm), dry, U.S.N.M. 112354, Natal, prob. S. Africa, from W. F. H. Rosenberg. (See Stephenson and Rees 1967a). Two ♂ (G54 F55.5 mm), U.S.N.M. 72540, Yenosima, mouth of Bay of Jeddo, Japan, coll. E. S. Morse, 594 Boston Soc. Nat. Hist. One ♀ ovig (39 mm), U.S.N.M. 72533, Yenosima, mouth of Bay of Jeddo, Japan, coll. E. S. Morse, 595 Boston Soc. Nat. Hist. One ♀ (35 mm), U.S.N.M. 45882, Wakanoura, Kishu, Japan, exchanged Imper. Univ. Tokyo. One ♂ (77 mm); one ♀ (53 mm), U.S.N.M. 26254, Nakanoura, Kū, Japan, Jordan and Snyder, 1900, Stanford Univ. One juv. (6 mm), U.S.N.M. 39801, between Koh Riat and Koh Mesan, Gulf of Siam 7.ii.1900, 3–5 fms, coll. Th. Mortensen. One ♂ (19.5 mm), U.S.N.M. 112423, Shimizu, Suruga, Japan, 'Albatross', 14.x.1906, shore. (Previously identified as *P. pseudoargentatus* Stephenson; see Stephenson and Rees 1967a). One ♀ (35 mm), U.S.N.M. 54519, Yamagata Prefecture, Japan, August 1917, coll. M. Sasaki, badly damaged. One ♂ (37 mm), U.S.N.M. 60250, Toyama Bay, Honshu, Japan, from Hokkaido Imperial University, coll. M. Sasaki 1925. One ♂ (25 mm), U.S.N.M. 112434, Lembah Strait, Celebes, Philippines, 14.vi.1929, coll. Herre. (Previously identified as *P. pseudoargentatus* Stephenson; see Stephenson and Rees, 1967a). Two ♀ (51 mm), U.S.N.M. 127068, Indian Ocean, 9° 13'N., 95° 51'E., 23.iii.1963, 60–50 fms, Anton Bruun sta. AB-20 cruise 1, Indian Ocean Exped. 'Anton Bruun', 31.vii.1963. One ♂ (32 mm), U.S.N.M. 127069, Indian Ocean, 17° 41'N., 71° 33'E., to 17° 45'N., 71° 32'E., 14.xi.1963, 90 fms, Anton Bruun. (This specimen has a distinctly swollen branchial region but no trace of parasites is evident.)

Universitets Zoologiske Museum, Copenhagen: One ♂ (72 mm), dry, Tranquebar, Daldot (Fabricius, 1798 type). Two specimens (45 and 54 mm), photographs only, Tranquebar, Daldot (Fabricius original). One ♀ (ca 19 mm), Singapore, 4.vi.1903, low water. One ♂ (18 mm), off Jola, Philippines, 19.iii.1914, ca. 25 fms, sand, coll. Th. Mortensen. (Previously identified as *P. pseudoargentatus* Stephenson; see Stephenson, 1972a). One ♀ (24.5 mm), Misaki, 26.iv.1914, ca. 3 fms, coll. Th. Mortensen. (Previously identified as *P. gladiator* Stephenson and Campbell; see Stephenson, 1972a). One ♂ (18 mm), Misaki, ca. 10 fms, Grus, 30.iv.1914, coll. Th. Mortensen. (Previously identified as *P. gladiator* Stephenson and Campbell; see Stephenson, 1972a). One ♂ (18.5 mm), Misaki, 9.vi.1914, ca. 25 fms, sand, coll. Th. Mortensen. One ♂ (30 mm), Sunda Strait, Dan Kai Is. Exped. sta. 75, 6° 10'S., 105° 44'E., 29.vii.1922, 40 m, sand and shells. One ♂ (18 mm), Java Sea, Dan Kai Is. Exped. sta. 118, 7.viii.1922, 27 m, sand and shell, Sigsbee trawl. (Previously identified as *P. pseudoargentatus* Stephenson; see Stephenson, 1972a). One ♂ (56.5 mm), 1½ miles east of Tanjong Rhu, off Singapore, Galathea sta. 346, 23.v.1951, 14 m, sand and mud, 1530–1600 hrs. Four ♂ (41–80 mm) and two ♀ (51–61 mm), West Malay Peninsula, Thai Dan. Exped. just after sta. 1023, 14.i.1966. D One ♂ (36.5 mm) and two ♀ (35–39.5 mm), West Malay Peninsula, Thai. Dan. Exped. sta. 1153, 9° 12'N., 98° 15'E., 5.iii.1966, 17 m, fine sand. One ♀ (55 mm), West Malay Peninsula, Thai. Dan. Exped. sta. 1171, 9° 13'N., 97° 50'E., 7.iii.1966, 70 m, mud with

many large shells. One ♂ (61.5 mm), West Malay Peninsula, Thai. Dan. Exped. sta. 1179, 8° 08'N., 98° 17'E., 9.iii.1966, 18 m, sandy mud.

Western Australian Museum: Three ♂ (28–62 mm, C = 54 mm); one ♂ with *Sacculina* (ca. 29 mm); one ♀ (37 mm) and one ♀ ovig (47 mm), W. A. M. 111–71, Ceylon with consignment from Mullaitivu Mud Banks, coll. G. H. P. De Bruin. H One ♂ (63 mm) W.A.M. 50–60, 5 miles NW. Gun Island W.A., Southern group Abrolhos Is. 11.v.1960, 30–35 fms, coral rubble, sponge and weed, coll. R. W. George on 'Davena'. (Holotype of *P. pseudoargentatus* Stephenson; see Stephenson, 1961). One ♀ with *Sacculina* (47 mm), W.A.M. 101–71, near Siasi Is., Sulu Arch., 17.ii.1964, sand, coll. B. R. Wilson on 'Pele'.

APPENDIX 2

SPECIMENS PREVIOUSLY IDENTIFIED AS *Portunus gladiator* FABRICIUS.

Portunus argentatus (A. Milne Edwards): One ♀ (18.5 mm), W.A.M. 103–71, NW. of Bluff Pt., Geraldton, W.A., 27° 40'S., 113° 03'E., 36 m, C.S.I.R.O. sta 131, 22.viii.1963. Two ♂ immature (15 mm), W.A.M. 107–71, NW. of Carnarvon, W.A., 24° 00'S., 112° 51'E., 130 m, C.S.I.R.O. sta 29, 2.ii.1964.

Portunus brockii (de Man): Three ♂ (21.5–27 mm) and two ♀ (15–23 mm), U.S.N.M. 73153, Iloilo, Panay Id., Philippines, coll. H. C. Kellers, March–May 1929.

Portunus gracilimanus (Stimpson): One ♀ (18 mm) and one ovig. ♀ (19.5 mm), W.A.M. 110–71, Coronado Bay, Mindanao, Sulu Sea, 46–130 m., sand and mud, coll. M. King on 'Pele', 10.ii.1964. One ♂ (40 mm), W.A.M. 104–71, Gulf of Carpentaria Prawn Survey, sta. 1541, coll. R. W. George on 'Rama', November 1964. One ♂ (27 mm), W.A.M. 106–71, Ceylon, with a consignment from Mullaitivu Mud Banks, coll. G. H. P. de Bruin.

Portunus granulatus (H. Milne Edwards): Five ♂ (15–26 mm) and six ♀ (21.5–30.5 mm), U.S.N.M. 75885, Benkulen, Sumatra, coll. H. C. Kellers, November 1925.

Portunus rubromarginatus (Lanchester): One ♀ (42 mm), W.A.M. 109–71, Shark Bay, W.A., 17 m, coll. E. Barker, 18.x.1964. One ♀ (45 mm), W.A.M. 108–71, Shark Bay, W.A., coll. W. and W. Poole Bros., August 1965. One ovig ♀ (47 mm), W.A.M. 105–71, Shark Bay, W.A., coll. A. McKenzie, August 1965. One ♂ (40 mm) and two ♀ (36.5–38.5 mm), A.M. P.16826, ½ mile S. of western end of One Tree Island reef, Capricorn Group, Great Barrier Reef, Queensland, 50 m, sand and shell, coll. J. Paxton and B. Goldman, 5.ii.1969.

FROGS OF THE GENUS *TAUDACTYLUS* WITH DESCRIPTIONS
OF TWO NEW SPECIES (ANURA: LEPTODACTYLIDAE)

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ABSTRACT

Two new species of *Taudactylus* are described, and the status of *T. diurnus* and *T. acutirostris* are reviewed. The genus *Taudactylus* now contains four species, *T. acutirostris* (Anderson), *T. diurnus* Straughan and Lee, *T. eungellensis* sp. nov., and *T. rheophilus* sp. nov., and ranges along the Great Dividing Range of Queensland. Extension of ranges of *T. acutirostris* and *T. diurnus* are mentioned; *T. rheophilus* is found only on Mt Lewis, N. Queensland and *T. eungellensis* at Eungella and Finch Hatton, central eastern Queensland. *T. rheophilus* is characterized by the broad head, and vertical snout in profile, and *T. eungellensis* differs from *T. diurnus* by the larger size and the male call. It is suggested that this genus was derived in the Tertiary, from *Crinia*-like ancestors, which adapt to mountain rainforest habitat. This genus now survives as a relict in mountain rainforest pockets along the Great Dividing Range of Queensland.

In 1966, I. R. Straughan and A. K. Lee erected a new genus *Taudactylus* for a moderate sized leptodactylid frog with T-shaped terminal phalanges. *Crinia acutirostris* also has the T-shaped terminal phalanges and toes, hence it was placed in the genus *Taudactylus* (Straughan and Main, 1966). Lynch (1971) redefined the genus *Taudactylus* and presented a series of osteological characters, however only the T-shaped terminal phalanges of toes and fingers are diagnostic of this genus; Lynch also synonymized *T. diurnus* Straughan and Lee and *T. acutirostris* (Anderson) without presenting any concrete evidence, hence considered this genus monotypic.

The object of this paper is to describe two new species which belong to the genus *Taudactylus*, to clarify the taxonomic status of *T. acutirostris* and *T. diurnus*, and to present the biology and the distribution of members of this genus.

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MATERIALS AND METHODS

Dissection of the myology was done under a Wild Stereoscopic microscope; dried as well as cleared and stained skeletons were prepared. Measurements were taken with dial calipers with an accuracy of 0.1 mm. Drawings were done by the senior author under a stereo-microscope with the aid of a camera lucida. The following abbreviations were used for adult measurements: SV, snout-vent length; TL, tibial length; HW, head width at broadest part; EN, distance between external nostril and anterior border of eye; IN, straight distance between the two external nostrils. For tadpoles the following abbreviations of measurements were used: ST, snout-tail length; SV, snout-vent length; TAL, tail length measured from tip of tail to anal opening; TH, tail height at broadest portion; BW, body width at broadest section. The following are the abbreviations of Institutions where the specimens are deposited: AM-Australian Museum, FMNH-Field Museum of Natural History, QM-Queensland Museum, WAM-Western Australian Museum, DSL-David S. Liem collection.

SYSTEMATICS

Recently, two species of leptodactylids were collected, one from North Queensland and another from Eungella-Finch Hatton area, central eastern Queensland. These two specifically distinct forms show great similarities to the genus *Taudactylus*. Many characters shared by these four species are unique among the currently recognized leptodactylids: T-shaped terminal phalanges of digits; discs on tip of digit with longitudinal groove; sharp angular canthus rostralis; and that the M. geniohyoideus medialis ventral to M. geniohyoideus lateralis, lateral to M. sternohyoideus and inserting on distal half of posterior lateral process of hyoid plate. The above characters indicate a close relationship among the four species mentioned and clearly distinguish them as a group from any genus of Australo-papuan leptodactylids. On the basis of these distinctions, these two new species, *T. rheophilus* and *T. eungellensis*, are here referred to the genus *Taudactylus*.

Of 17 characters presented in the description of the new genus *Taudactylus* (Straughan and Lee, 1966) only two are diagnostic of the genus amongst the Australo-papuan leptodactylids, i.e. T-shaped terminal phalanges of digits, and the expansion of the digits distally into a disc. Lynch (1971) listed 33 characters in the diagnostic definition of this genus but only one is restricted to this genus i.e. T-shaped terminal phalanges. Omosternum was reported absent by Lynch (1971), however, after careful examinations the senior author found that it was absent in *Taudactylus diurnus* and *T. eungellensis* only, and present in *T. acutirostris* and *T. rheophilus*. The senior author agrees with Straughan and Lee (1966) that the fronto-parietal fontanelle is absent in *Taudactylus diurnus* contrary to Lynch's (1971) statement but the vomers are minute elongated bones on the median side of the choanae and are present in *T. diurnus* as well as *T. acutirostris* and thus agree with Lynch's, but not with Straughan and Lee's statement. The nasal bones are variable, with moderate size club-shaped nasals moderately separated from each other in *T. diurnus*, and small narrow nasal bones widely separated from each other in *T. acutirostris*, *T. eungellensis* and *T. rheophilus*. All other characters agree with Lynch's (1971) and Straughan and Lee's (1966) descriptions.

In this paper only the above characters and those which are diagnostic of the genus *Taudactylus* are listed in the generic account.

The following measurements were recorded for adult frogs: SV, HW, TL, SL, EN, IN, and the HW/SV, TL/SV, and EN/IN ratios were calculated. Only the SV-length, and HW/SV ratio are useful for differentiating members of the genus *Taudactylus*. For tadpoles the ST, SV, TAL, TH, and BE and TAL/ST, TH/TAL, and BW/SV ratios were recorded. Only BW/SV ratio is useful for distinguishing between *T. acutirostris* on one hand and *T. diurnus* and *T. eungellensis* on the other.

***Taudactylus* Straughan and Lee, 1966**

Taudactylus Straughan and Lee, 1966, p. 63 (Type-species by original designation, *Taudactylus diurnus* Straughan and Lee, 1966); Straughan and Main, 1966, p. 11; Lynch, 1971, p. 95.

DIAGNOSIS: This genus could be distinguished from any other Australo-papuan leptodactylid frogs by the following characters: T-shaped terminal phalanges of fingers and toes (Fig. 3D); M. geniohyoideus medialis ventral to geniohyoideus lateralis, lateral to M. sternohyoideus and inserting on distal half of the posterior lateral process of hyoid plate (Fig. 2B); characterised externally by expanded digital discs with a median longitudinal groove dorsally (Fig. 5), sharp canthus rostralis and in some wedge-shaped snout protruding beyond mouth. Tadpoles of *T. diurnus*, *T. eungellensis* and *T. acutirostris* could easily be distinguished from any other Australo-papuan tadpoles by the presence of broadly expanded umbrella-shaped lips forming a sucker mouth, and the presence of lateral line organs on head and body. The labial tooth rows are absent in *T. diurnus* and *T. eungellensis* and present in *T. acutirostris*, with a formula of I, 1/1, I, I(1/4).

CONTENT: Four species: *Taudactylus acutirostris* (Anderson), *Taudactylus diurnus* Straughan and Lee, *Taudactylus eungellensis* sp. nov., and *Taudactylus rheophilus* sp. nov.

DESCRIPTION AND VARIATION: All members of the genus *Taudactylus* are moderate sized frogs, males range 21.0–27.2 mm and females 21.0–35.9 mm in SV-length; TL/SV ratio is 0.435–0.565; HW/SV ratio is 0.288–0.412; EN/SL ratio 0.390–0.658; EN/IN ratio is 0.525–0.773. Snout in profile protrudes beyond upper jaw in *T. acutirostris*, *T. diurnus* and *T. eungellensis* and in dorsal aspect acuminate or blunt (Fig. 4A, B). Loreal region straight, canthus rostralis form a sharp angle in section. Tongue 1.5 to 1.25 longer than wide, free posteriorly. Vomerine teeth absent. Vocal sac and its opening variable in occurrence. Pupil oval and orients horizontally. Tympanum hidden under the skin. Dorso-lateral skin fold and three tubercles arranged in a triangle on the lower back are present in *T. acutirostris* only. Dorsal skin of *T. diurnus* and *T. eungellensis* is coarsely granular with round tubercles whereas *T. acutirostris* is finely granular with longitudinal skin folds. Cloacal opening is directed posteriorly or posteroventrally at mid-level of the thighs.

Nuptial pad variable in appearance and occurrence. Digits unwebbed and distally expanded into discs with a longitudinal groove (Fig. 5). Subarticular tubercle of fingers are variable in occurrence, but the metacarpal and palmar tubercles are always present.

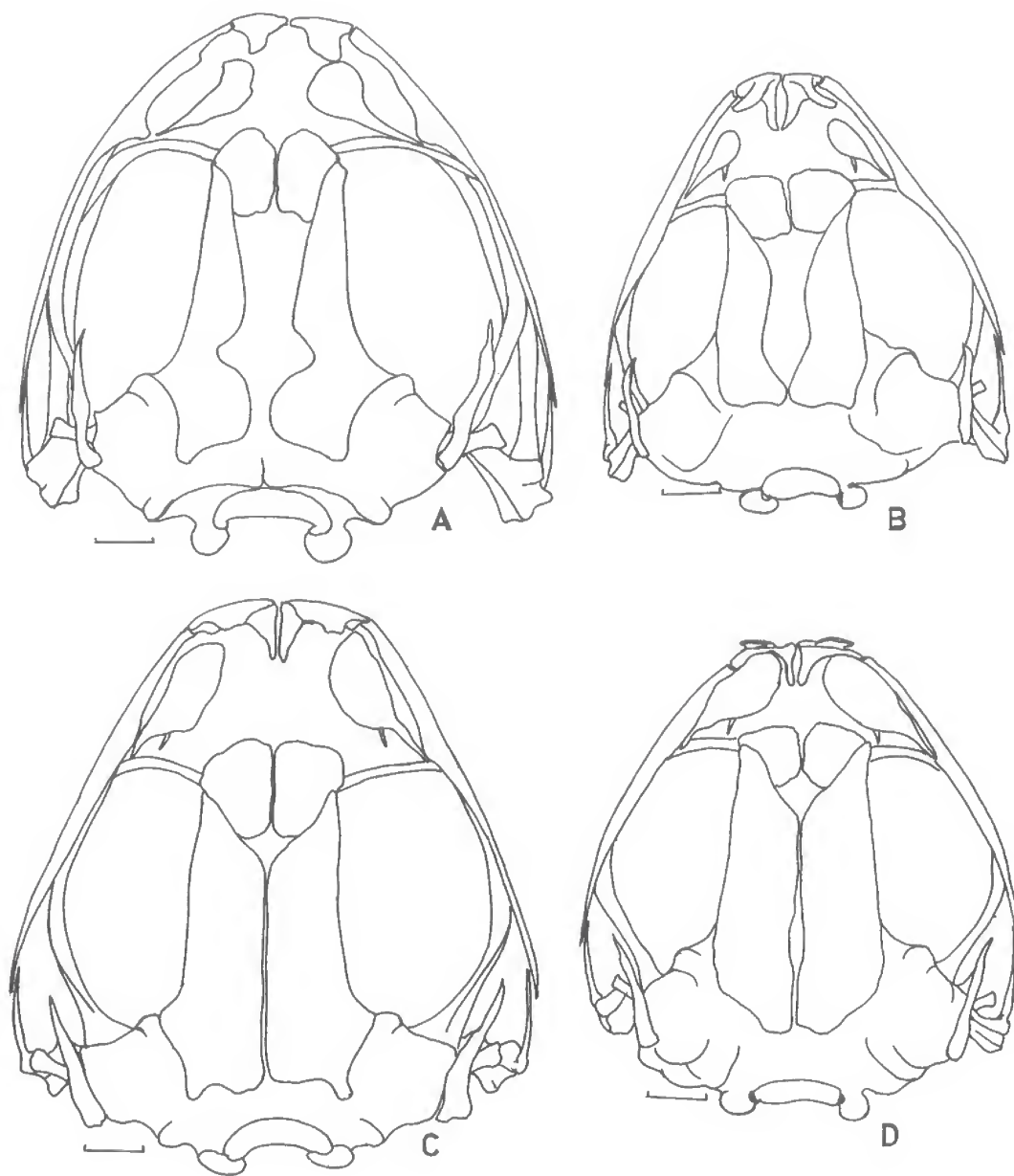


FIG. 1: A. Dorsal aspect of the skull of *Taudactylus rheophilus*.
B. Dorsal aspect of the skull of *T. acutirostris*.
C. Dorsal aspect of the skull of *T. eungellensis*.
D. Dorsal aspect of the skull of *T. diurnus*.

Toes unwebbed, but with distinct toe fringes. Subarticular and plantar tubercles of toes are always present. Only the inner metatarsal tubercle is present. Phalangeal formula of fingers 2-2-3-3 and of toes 2-2-3-4-3.

OSTEOLOGY: Only the diagnostic, and corrected characters and those which have not been mentioned previously will be presented below, for all other osteological data see Lynch (1971). Fronto-parietal fontanelle may be present or absent; nasal variable in size; sphenethmoid divided; length of zygomatic rami of squamosal variable; vomerine bone narrow on median border of choanae, vomerine teeth absent; maxilla toothed; pedicellate teeth; 8 presacral vertebrae, connected with intervertebral discs; cotyles of cervical vertebrae are widely spaced; 1st and 2nd vertebrae free; sacral vertebrae with expanded diapophyses, urostyle with two condyles; cricoid does not form a complete ring ventrally; median frenulum chordiae vocalis of larynx absent; alary process broad, wing-like (Fig. 2A); pectoral girdle arciferous; sternum cartilaginous, variable in shape; omosternum present or absent; carpals consists of a radiale, ulnare, naviculare, 1st, 2nd and 3rd carpale and a large fused bone consisting of 4th carpale and postaxial centrale; prepollex pointed; 1st, 2nd and 3rd tarsale as well as the prehallux present.

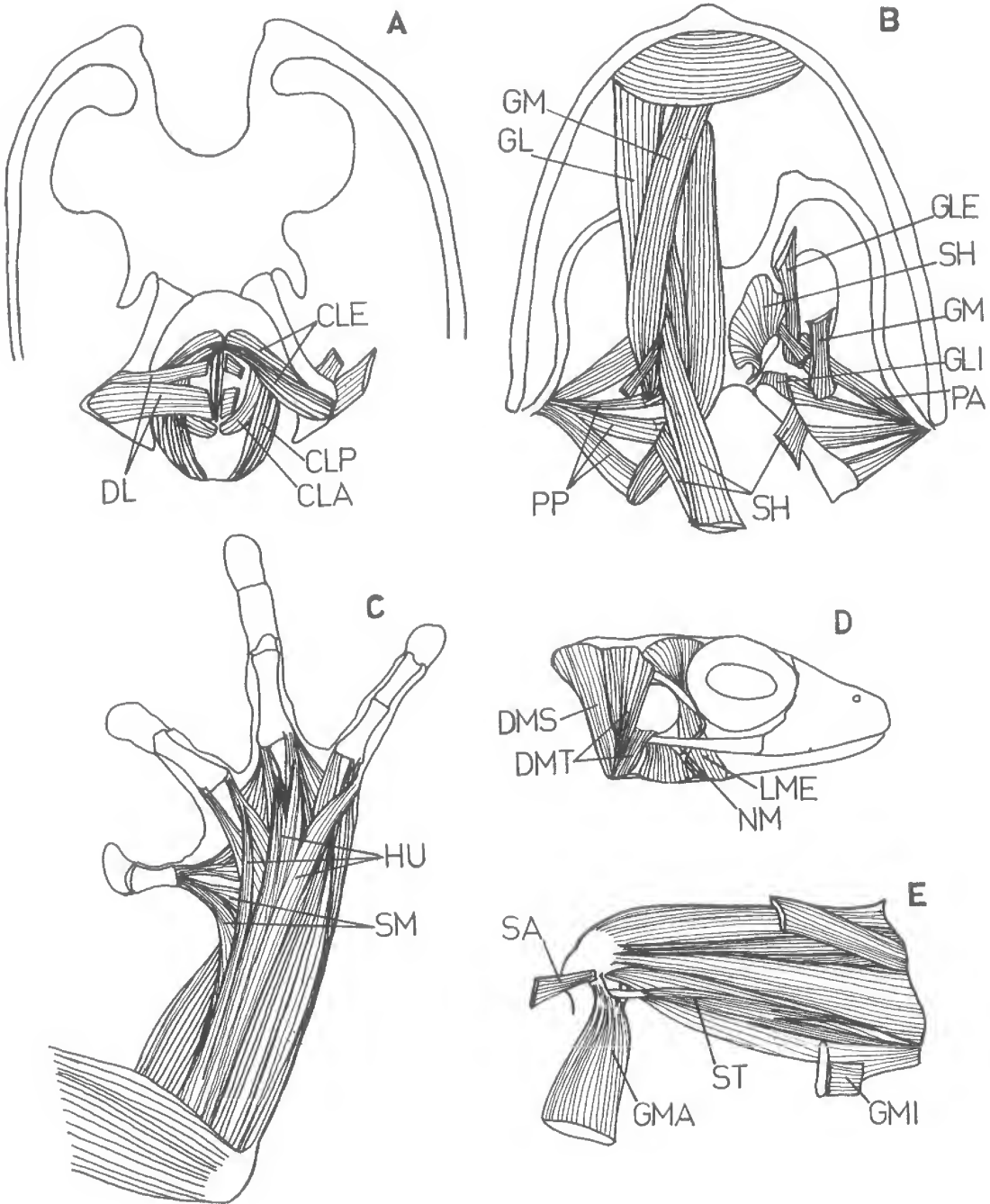
MYOLOGY: Depressor mandibulae consists of two main slips, a slender pars scapularis originating from the scapula and a strong pars tympanicus which originates from the squamosal, and posterior surface of prootic, and a short slender slip from the auditory capsule; M. levator mandibulae subexternus absent; nervus mandibulae is superficial and lies lateral to the M. levator mandibulae externus (Fig. 2D); M. supracoroideus profundus and superficialis are not fused; M. omohyoideus present inserting midway between base of posterior lateral process and the manubrium of the hyoid apparatus; M. geniohyoideus medialis is ventral to the geniohyoideus lateralis and inserts on distal half of posterior lateral process of the hyoid plate; M. geniohyoideus lateralis externus inserts on proximal portion of posterior lateral process and the internus on the proximo-medial third or two-thirds of thyrohyal; M. sterno-hyoideus dorsalis is free from the ventralis and inserts on proximo-lateral third of thyrohyal; pars medialis and lateralis of M. sterno-hyoideus lateralis are distinct, the former inserts on the base of hyale, curves medially toward midline, and then curves laterally to end at base of posterior lateral process, whereas pars lateralis inserts on the hyoid plate just lateral to medialis, but restricted along its middle third; M. hyoglossus consists of one pair of muscles; M. petrohyoideus anterior inserts on base of alary process, lateral to insertion of M. sterno-hyoideus ventralis; three slips of M. petrohyoideus posterior all inserting on dorsal surface of thyrohyal (Fig. 2B); M. dilatator laryngis consists of two slips in *T. rheophilus* (Fig. 2A) and only one slip in *T. diurnus*, *T. eungellensis* and *T. acutirostris*; M. constrictor anterior consists of one slip; apical elements of M. submaxilaris absent; distally the M. humerodorsalis fragmented into the first, second, third, fourth phalangeal slip, and the fourth metacarpal slip in *T. diurnus*, *T. eungellensis* and *T. acutirostris*, whereas the first is absent in *T. rheophilus* (Fig. 2C); M. externus digitorum brevis superficialis of 2nd finger originates from the ulnare; M. supinator manus with two slips, one originates from dorso-lateral surface along mid one-third of radio-ulna, and another from disto-lateral surface of humerus, both join together distally to insert on dorsal surface halfway down

the first finger (Fig. 2C); *M. palmaris longus* is entire; *tendo superficialis* of the 2nd, 3rd and 4th fingers originate from the aponeurosis palmaris; *M. adductor longus* present; distal tendon of *M. semitendinosus* lies dorsal to (*T. acutirostris*, *T. rheophilus*, Fig. 2E) or pierces through *M. gracilis major* (*T. diurnus* and *T. eungellensis*); accessory slip of *M. semitendinosus* which joins the adductor magnus is absent; *M. extensor cruris brevis* lies medial to the *M. tibialis anticus brevis* and is as long as the entire length of the cruris; *M. tibialis anticus brevis* slender, originates on proximo-lateral fourth of cruris, and inserts on proximo-dorsal surface of tibio-fibulare fusion; *M. extensor digitorum communis longus* consists of a single slip, joins with the distal tendon of the extensor brevis superficialis of the 4th toe to insert on the disto-dorsal portion of the metatarsal of the 4th toe; a tendinous tissue which originates from the aponeurosis plantaris joins the formation of the *tendo superficialis* of the third toe; accessory slip of the *M. abductor brevis plantaris hallucis* absent; *M. abductor prae hallucis dorsalis* is short, inserting on postero-dorsal surface of the prehallux; the ventralis inserts on the posterior surface of the basal segment of the prehallux; the *M. lumbricalis longus digiti* of the 2nd toe absent; *M. extensor brevis superficialis* of 5th toe absent; all three slips of *M. extensor brevis medii* supplying the 1st, 2nd and 3rd toes are present.

EGGS AND TADPOLES: Eggs are relatively large, 2.2–2.6 mm in diameter, encapsulated individually with a clear gelatinous capsule up to 4.6 mm in diameter. In *T. diurnus*, *T. eungellensis* and *T. acutirostris*, egg masses consist of 2–3 dozen eggs deposited under rocks in creeks. Tadpoles have a dextral anal opening, sinistral spiracle, and are characterized by the umbrella-shaped labium forming a sucker mouth, distinct lateral line organs on head and body, weak jaws; labial tooth rows are absent in *T. diurnus* and *T. eungellensis*, but present in *T. acutirostris*.

REMARKS: All members of the genus have distinct lateral fringes, as do *Crinia haswelli*, *C. sloanei* and *C. riparia*; lack of the outer metatarsal tubercles is shared with *Crinia darlingtoni*, *C. haswelli*, *C. laevis*, *C. leai*, *C. rosea*, and *C. victoriana*. All members have maxillary teeth as in *Crinia*; absence of vomerine teeth is shared with the majority of myobatrachines. Mature males of *Taudactylus* have dark brown to black testes and this is shared with *Kyarranus* and *Crinia* amongst the Australo-papuan leptodactylids. All members of this genus are primarily diurnal and restricted along mountain rainforest creeks.

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- FIG. 2: A. Ventral aspect of the hyoid apparatus (note the expanded alary process), and ventral laryngeal muscles of *Taudactylus rheophilus*. CLA, constrictor laryngis anterior; CLE, constrictor laryngis externus; CLP, constrictor laryngis posterior; DL, dilatator laryngis.
- B. Ventral aspect of hyoid muscles of *Taudactylus diurnus*. GL, geniohyoideus lateralis; GLE, geniohyoideus lateralis pars externus; GLI, geniohyoideus lateralis pars internus; GM, geniohyoideus medialis; PA, petrohyoideus anterior; PP, petrohyoideus posterior; SH, sternohyoideus.
- C. Dorsal aspect of forearm muscles of *Taudactylus rheophilus*. HU, humerodorsalis; SM, supinator manus.
- D. Head muscles of *Taudactylus eungellensis*. DMS, depressor mandibulae pars scapularis; DMT, depressor mandibulae pars tympanicus; LME, levator mandibulae externus; NM, nervus mandibulae.
- E. Ventral muscles of the thigh of *Taudactylus rheophilus*. GMA, gracilis major; GMI, gracilis minor; SA, sartorius; ST, semi-tendinosus.



KEY TO SPECIES OF THE GENUS *TAUDACTYLUS*

1. Dorso-lateral skinfold present; three tubercles, each marked by a black blotch arranged in a triangle are present on the coccygeal area
 *Taudactylus acutirostris*
 Not as above 2
- 2(1). Head broad, HW/SV ratio more than 0.380; subarticular tubercles present on all fingers; snout vertical in profile (Fig. 4c) digital disc narrow, 1.25 times width of digits; male with a vocal sac, a pair of slit openings and subcutaneous nuptial glands on 1st and 2nd fingers; a distinct black and light irregular marking on the flank between base of forearm and groin
 *Taudactylus rheophilus*
 Not as above 3
- 3(2). Dorsum light background with distinct irregular dark markings; ventral surfaces of thighs immaculate cream or yellow, or only the antero and postero-distal portion of the thighs are dark spotted. Females reach up to 35.0 mm, males averaging 26.0 mm *Taudactylus eungellensis*
 Dorsum dark olive background, irregular dark marking hardly distinguishable; ventral surfaces of thighs greyish cream and heavily spotted; abdomen and throat generally with dark brown spots. Females reaching up to 30.0 mm, and males averaging 25.0 mm *Taudactylus diurnus*

***Taudactylus diurnus* Straughan and Lee**

(Figs. 1D, 2B, 3B,F, 4B, 5, 6)

Taudactylus diurnus Straughan and Lee, 1966, p. 63.

MATERIAL EXAMINED

HOLOTYPE: Adult male, QM J13398, from Green's Fall, Maiala National Park, Mt Glorious, Queensland, collected by I. R. Straughan, 12.v.1965.

PARATYPES: (28) 3 ♂, 4 ♀, 6 unsexed (3 juv) (QM J13399-411); 2 ♂, 4 ♀, (AM R24656-61); 3 ♂, 3 ♀, (WAM R26337-42).

OTHER MATERIAL.—(70) Mt Glorious, SE Queensland, 18 ♂ (DSL 1083-4, 5128, 5130, 5134-5; 5264, 5266-7, 5395, 5399, 5400-1, 5404-7, 5409), 21 ♀ (DSL 3084-5, 5121-7, 5131-3, 5136-7, 5140, 5271, 5396, 5402-3, 5411); Kondallilla, SE Queensland, 13 ♂ (DSL 5944-5, 5949-50, 5955-8, 5961; 6240-3), 8 ♀ (DSL 5946-7, 5953, 5959-60, 5962), 9 juveniles (DSL 5943, 5948, 5951-2, 5954, 6239, 6244, 6247-8). Skeleton (DSL 1086) and cleared specimen (DSL 1085) are from Mt Glorious, SE Queensland.

DIAGNOSIS: This species is characterized by the following combination of characters: absence of dorso-lateral skinfold; head narrow, HW/SV ratio 0.288-0.333; snout slightly protruding and sloping inward in profile; dorsal aspect of snout blunt; subarticular tubercle between phalanges of fingers absent; skin granular; vocal sac absent in males; one rounded dark grey nuptial gland present on medio-dorsal part of hand of breeding males; a short black stripe from behind eye to base of forearm, sometimes accompanied by another lighter band ventral to the first; width of toe fringes about 2/5 width of toe;

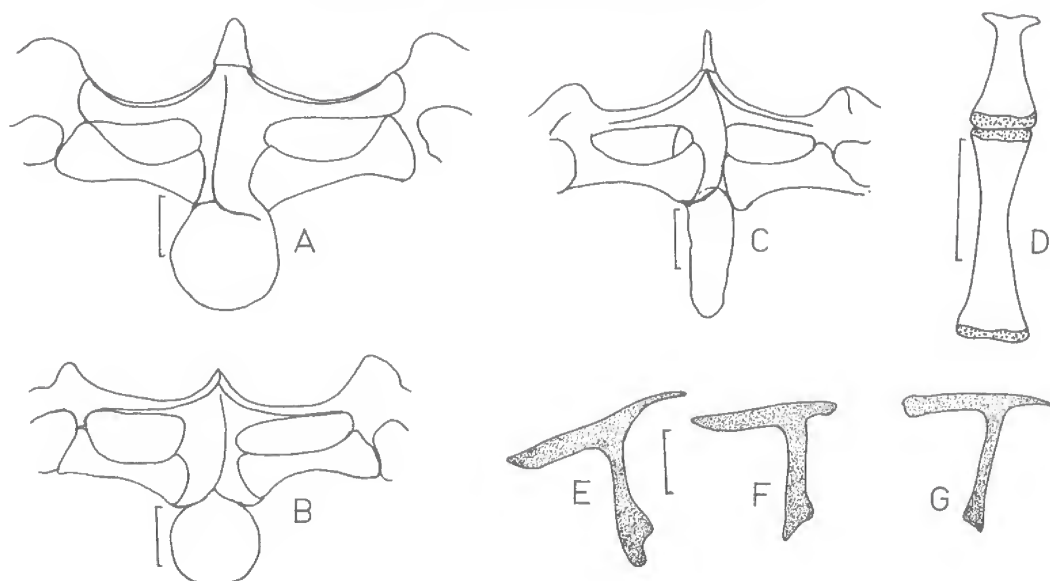


FIG. 3: A. Ventral aspect of the pectoral girdle of *Taudactylus rheophilus*.
 B. Ventral aspect of the pectoral girdle of *T. diurnus*.
 C. Ventral aspect of the pectoral girdle of *T. acutirostris*.
 D. Penultimate and terminal phalanges of the 4th toe of *T. eungellensis*.
 E. Lateral aspect of the squamosal of *T. rheophilus*.
 F. Lateral aspect of the squamosal of *T. diurnus*.
 G. Lateral aspect of the squamosal of *T. acutirostris*; right arm is the otic ramus.

disc of digits large, about 1.5 times width of neck of disc. It only differs from *eungellensis* by its smaller size, darker dorsal background colour and the heavily spotted ventral surfaces of the thighs.

DESCRIPTION AND VARIATION: The description of Straughan and Lee (1966) is sufficient, however it is noteworthy to add the following: This species is a moderate to large sized *Taudactylus* frog, males are 22.0–27.2 mm (mean 24.6 mm, $N = 31$), and females are 23.3–30.6 mm (mean 28.8 mm, $N = 29$) in SV-length; head narrow, HW/SV ratio 0.288–0.353; dorso-lateral skinfold absent; skin granular, subarticular tubercles of fingers absent; toe fringes broad, half the width of the toe; male with rounded dark grey nuptial pad on dorso-medial portion of hand; cross-bands on fore and hind limbs oriented at right angles to the longitudinal axis of the limbs; ventral surface of males white or grey with greyish brown spots on throat and pectoral region, ventral surface of females cream or yellowish and sparsely spotted with grey on throat and pectoral region. Nasal bones moderately large; vomerine bone very small; fronto-parietal fontanelle absent or just a narrow suture (Fig. 1D); zygomatic rami of squamosal one third length of otic rami (Fig. 3F); omosternum absent; sternum rounded (Fig. 3B).

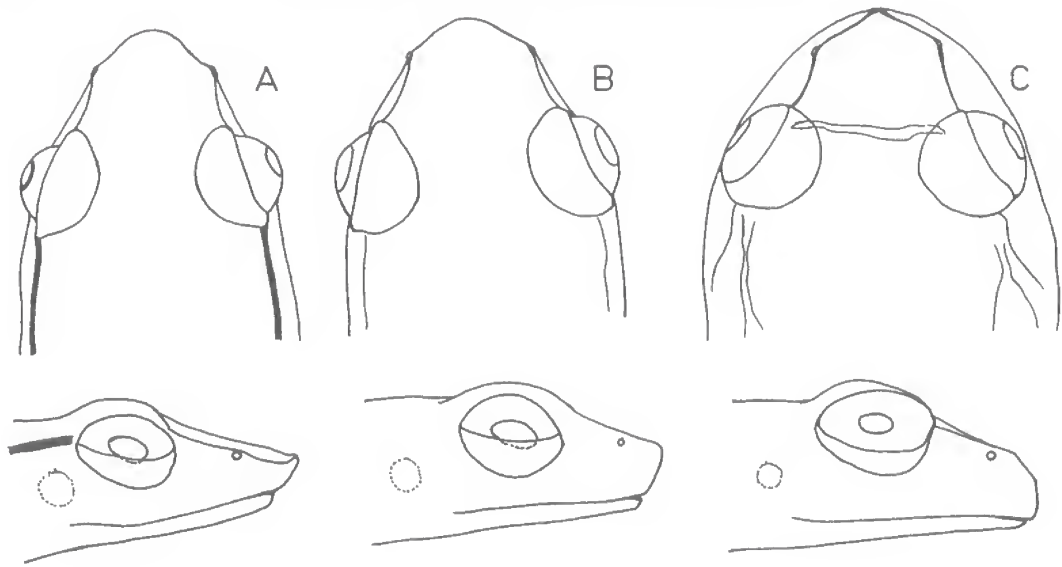


FIG. 4: A. Dorsal and lateral aspect of head of *Taudactylus acutirostris*.
 B. Dorsal and lateral aspect of head of *T. diurnus*.
 C. Dorsal and lateral aspect of head of *T. rheophilus*.

TADPOLES: Moderate sized tadpoles with rounded snout, rounded tail tip, dextral anus, sinistral spiracle, characterized by the absence of labial teeth and the umbrella-shaped lip, and with the labial papillae completely surrounding the labium (Fig. 6). Details of tadpoles are presented elsewhere (Liem, MS1).

BIOLOGY: Large eggs are deposited in gelatinous clumps under rocks in water in mountain creeks; tadpoles are bottom dwellers and scrape food from the substrate with their umbrella-shaped lip. Tadpoles and adults are sympatric and synchronopatric with *Adelotus brevis*, *Myxophyes fasciolatus*, *Hyla pearsoniana* and *H. lesueuri* on Mt Glorious, and with *Hyla lesueuri*, *H. chloris*, *H. pearsoniana*, *Mixophyes fasciolatus*, *Adelotus brevis* and another unnamed genus in Kondallilla, SE. Queensland. Breeding peak occurs between late November and late April, whereas tadpoles are found throughout the year. Amplexus is inguinal.

CALL: Contrary to Straughan and Lee (1966), it was found that the males of this species do call. Their call is a very soft chuckling sound repeated 1–2 or 4–5 times in quick succession. It is hardly audible in the field, probably because of its infrequent call and the loud background noises of rushing water current. The call could clearly be heard when males are placed in an aquarium in a quiet room. It takes about 4–5 minutes from one to the next call of one individual. Lack of a vocal sac may be the main cause of the softness of the call.

HABITAT: *Taudactylus diurnus* is restricted along the rocky mountain creeks in rain forest between 500–600 m above sea level on Mt Glorious, in wet sclerophyll forest between 400–500 m above sea level in Kondallilla, 100 km N. of Brisbane, SE. Queensland. This species prefers shady and permanent flowing mountain creeks. They were collected on rocks near water, on creek banks, as well as on rock ledges with seepage water. It clings with its toe discs on rock walls or on rocks in the creeks, and when disturbed it jumps into the water and stays on the bottom for up to 15 minutes.

In both localities this species is active only during the day time.

DISTRIBUTION: At present it is known from only 2 localities; i.e. Mt Glorious, and Kondallilla, 3 km SW. Montville, SE. Queensland.

REMARKS: Mt Glorious and Kondallilla populations are identical in all measurements and colouration. However SV length in both populations of *T. diurnus* is significantly smaller than in its closely related species *T. eungellensis* from Eungella-Finch Hatton area, central eastern Queensland.

***Taudactylus eungellensis* sp. nov.**

(Figs. 1C, 2D, 3D, 8)

MATERIAL EXAMINED

HOLOTYPE: Adult male, QM J22433, Eungella, 75km W. of Mackay, central eastern Queensland, 900m above sea level, collected by David S. Liem, 24.xi.1971.

PARATYPES: 5 ♂ (QM J22434–7, DSL 6053), 13 ♀ (QM J22442–9, DSL 60650, 6056, 6061, 6065, 6069), Finch Hatton Gorge, 60km W. of Mackay, central eastern Queensland, 19.v.1972; 2 ♂ (QM J22438–9), same locality, 24.xi.1971; 3 ♂ (QM J22440–1, DSL 4823), type locality, 19.xii.1971; 2 ♂ (DSL 5441, 6062), 5 ♀ (DSL 6049, 6055, 6058, 6073, 6076), 8 juveniles (DSL 6044–5, 6047–8, 6067, 6071, 6074–5), 3 skeletons (DSL 5940–1), type locality; 1 (DSL 4822), Finch Hatton Gorge, 60km W. of Mackay, central eastern Queensland. A total of 35 tadpoles of stages 25, 26, 27, 28, 30, 34, 38, 39, 40, and 42 from Eungella and Finch Hatton Gorge were examined. All paratypes were collected by David S. Liem.

DIAGNOSIS: *T. eungellensis* closely resembles *T. diurnus* and could be characterised as follows: dorso-lateral skinfold absent; head narrow, HW/SV ratio 0.285–0.341; snout protruding and sloping inward when viewed in profile; as in *T. diurnus* dorsal aspect of snout blunt or slightly rounded; subarticular tubercles of fingers absent; mature males with rounded nuptial pad on back of the hand; vocal sac absent in males; background colour of dorsum yellowish green, with distinct black colour markings; irregular X-shape marking on the back behind the head is characteristic to this species. This species could be distinguished from its closely related species, *T. diurnus*, by its larger SV length and the immaculate yellow ventral surfaces of abdomen and thighs. Generally the anal tubercles which are present on each side of the anal opening are more pronounced in *T. eungellensis*.

DESCRIPTION OF HOLOTYPE: SV length 26.0 mm; tibia length 14.5 mm, 0.558 of SV length; head width 8.6 mm, 0.331 of SV length; dorsal aspect of snout bluntly acuminate, slightly protruding and in profile sloping inward; EN length 2.4 mm; IN length 3.2 mm; loreal region slightly concave; canthus rostralis angular in section, forming a distinct angle at level of nostrils to converge anteriorly at tip of snout; pupil horizontally oval; tympanum hidden; tongue 1.25 as long as wide, widest half way down its length, posterior two-thirds of tongue free; choanae moderately large, round; vomerine teeth absent; vocal sac absent; fingers unwebbed, distally expanded into discs; longitudinal groove on disto-dorsal portion of disc present. Length of fingers from shortest to longest 1-2-4-3; phalangeal formula of hand 2-2-3-3; terminal phalanges of fingers and toes T-shaped; metacarpal tubercles present on all metacarpo-phalangeal joints; subarticular tubercles absent; lateral palmar tubercle rounded and twice that of the oval inner one; mature males with greyish finely spinulated rounded nuptial pad on back of hand at base of 2nd and 3rd finger; toes not webbed, but broadly fringed; fringe width up to half width of toe; distally the toes are expanded into discs with longitudinal groove; length of toe from shortest to longest 1-2-3-5-4, and phalangeal formula from 1st to 5th toe, 2-2-3-4-3; metatarsophalangeal tubercles on base of toes ovoid; inner metatarsal tubercle ovoid; outer one absent.

Skin of dorsum chagreen with tubercles; a distinct conical tubercle present on postero-dorsal portion of thigh on each side of cloaca; postero-medial portion of thighs heavily granular; throat, abdomen, and ventral surfaces of thighs and tibia smooth; cloacal opening ends along a tube directed downward at mid level of thighs. Dorsal ground colour yellowish tan with rich irregular dark brown or black markings; broad interorbital transverse band crosses head, with two others anterior to this; the back is marked with an irregular X-shaped marking; coccygeal region with irregular dark markings; black band runs from behind the eye to the base of the forearm; flank with irregular dark markings; forelimbs with 3 dark crossbands; fingers crossbanded, 3 dark cross bands on the 3rd finger; 3 dark cross bands on dorsal surfaces of thighs, 2 broad and 2 narrow cross bands on tibia, 2 cross bands on the heel; 3rd and 5th toes crossbanded, whereas the 3 inner toes are immaculate yellowish. Throat and abdomen immaculate cream coloured; ventral surfaces of fore-limbs, thighs, tibia and tarsus bright yellow.

DESCRIPTION AND VARIATION: Seven males, 25.0–28.0 mm (mean 25.9 mm) and 24 females, 27.6–35.9 mm (mean 31.2 mm) in SV length; TL/SV ratio 0.465–0.541 in males, 0.435–0.558 in females, 0.488–0.593 in juveniles. HW/SV ratio 0.285–0.341 in males, 0.290–0.331 in females, 0.316–0.346 in juveniles; EN/IN ratio 0.641–0.839 in males, 0.525–0.788 in females, 0.580–0.833 in juveniles. Females are significantly larger than males, and mature males can easily be distinguished from the females by the presence of a dark rounded nuptial pad on the back of the hand. Some individuals collected from Eungella are dark and the dorsal dark colouration is vaguely distinguishable; ventral surfaces of body and limbs of these dark individuals are bright yellow, spotted with dark brown spots on the throat and disto-ventral surfaces of the thighs. Colour markings are more pronounced in juveniles and in some individuals ventral dark blotches extend from the throat to half way down the abdomen. Males without vocal sac; mature males easily

distinguished by the dark roundish nuptial pad on dorsal surface of hand. Nasal bones moderately broad, widely separated from each other and not touching the sphenethmoid; fronto-parietal fontanelle absent (Fig. 1C); zygomatic rami of squamosal about $\frac{1}{3}$ – $\frac{1}{2}$ as long as that of the otic rami; omosternum absent; sternum rounded.

CALL: High pitched metallic tinkering noise, which sounds like a little hammer tapping a metal plate repeated 4–5 times in quick succession. The high pitched metallic sound of *T. eungellensis* could easily be distinguished by ear from the hardly audible *T. diurnus* call, and from the moderate tapping sound of *T. acutirostris*.

BIOLOGY: *T. eungellensis* differs from *T. diurnus* in that the former is active during the day as well as at night. Males were heard calling during the day as well as at night, some females were collected while foraging at night. They are found along small rainforest mountain creeks (Eungella) as well as in boulder strewn streams at Finch Hatton. Males call from under rocks and crevices in shady places along the creeks, whereas the females are found almost everywhere hopping on rocks and boulders along the creeks and streams. As in other *Taudactylus* species, when disturbed they escape into the water and remain submerged on the bottom for a considerable length of time. Large eggs measuring 2.2–2.6 mm in diameter, numbering 30–50 in an egg mass, are deposited under rocks in the water. Several egg masses were found in December. Males were heard calling in November and December as well as in May. Tadpoles are found in November, December and May. Numerous juveniles were observed and collected in May. From this evidence the breeding peak of this species is probably in summer. Amplexus is inguinal.

TADPOLES: As in *T. diurnus*, tadpoles of *T. eungellensis* are characterized by the umbrella-shaped lips, weak narrow keratinized jaws, absence of labial teeth, dextral anal opening, and left spiracle. Lateral line organs appearing as dots are present surrounding the eye, extending posteriorly behind the eye and forked into two branches, one leading toward the anal region and another extending along the muscular tail. Tail tip is rounded. There are no differences in measurements and ratio between *T. eungellensis* and *T. diurnus* tadpoles. Tadpoles of *T. eungellensis* differ from *T. diurnus* in the prominent X-shaped marking on the dorsal side of the body and the distinct papillar ridges on the lower labium (Fig. 8), comprising an inverted V-shaped outer ridge, and a pair of ridges at each side of the former which orient toward the mouth opening when at rest and lie parallel to the jaws when the mouth is forced open. Apparently these ridges are the degenerated labial tooth rows of the ancestral forms. Tadpoles of *T. eungellensis* and *T. diurnus* differ from *T. acutirostris* by the narrower body, absence of labial tooth rows, and the continuous row of labial papillae forming a complete umbrella-shaped lip. As in tadpoles of the other known species, they are bottom dwellers in fast running water as well as in rock pools. *T. eungellensis* is synchronopatric with *Hyla lesueuri* and *H. chloris*.

HABITAT: This species is found along small creeks in the rain forest (Eungella, Finch Hatton Gorge), as well as in wet sclerophyll forest (Finch Hatton Gorge, central Queensland). The vertical distribution ranges from 500–900 m above sea level.

DISTRIBUTION: At present it is only known from Eungella, 75 km W. of Mackay, and Finch Hatton Gorge, 60 km W. of Mackay, central eastern Queensland.

ETYMOLOGY: The specific name refers to the locality, Eungella, where the holotype was collected. The name Eungella is of aboriginal origin meaning 'Land of the cloud'.

***Taudactylus acutirostris* (Anderson)**

(Figs. 1B, 3C,G, 4A, 5, 7)

Crinia acutirostris Anderson, 1916, pp. 1–20, 1 pl.; Parker, 1940, p. 83.

Taudactylus acutirostris: Straughan and Main, 1966, p. 11.

HOLOTYPE: 1 ♂, 1 ♀, Malanda, North Queensland, collected by Dr E. Mjoberg, 1910–1913.

MATERIAL EXAMINED: (57) North Queensland: 24 ♂ (DSL 5983, 5985, 5997, 5999, 6000, 6002, 6004–11, 6028, 6020–2, 6031, 6034–5, 6037, 6039 and 6041), 5 ♀ (DSL 5984, 6013–4, 6016, 6032), Mt Lewis; 7 ♂ (DSL 4801–7), 2 ♀ (DSL 4809–10), Speerwah; 2 ♂ (DSL 4812, 4815), 4 ♀ (DSL 4813–4, 4817–8), 1 juvenile (DSL 4816), 15 km S. of Mareeba; 1 ♂ (DSL 5987), 1 ♀ (DSL 5988), Tully's Falls; 4 ♂ (DSL 5989–92), Charmillan Creek, 10km N. Tully's Falls; 3 ♂ (DSL 5993–5), Tschooratypa Creek, Palmerston N. P.; 1 ♀ (DSL 6192), Kuranda; 1 ♀ (DSL 5986), Jullaten, Mt Molloy; 1 ♀ (DSL 3080), Malanda; 31 tadpoles, Mt Lewis and Tully's Falls, of stages 25–27; skeleton (DSL 4807), Speerwah; cleared specimen (DSL 4218), Kuranda.

DIAGNOSIS: Distinct light dorso-lateral skinfold; three tubercles arranged in a triangle on the posterior part of the back; wedge shape snout curved upward in profile. Dorsum immaculate brown meeting along a sharp line the black lateral colour which extends from behind the eye to the groin; ventral surfaces of body brownish cream to reddish (cream white in preservative) with extensive irregular dark blotches and markings; a relative broad cream marking runs along the margins of the throat. Head narrow, HW/SV ratio 0.301–0.351; fringes of toes narrow, $\frac{1}{4}$ – $\frac{1}{3}$ width of toe.

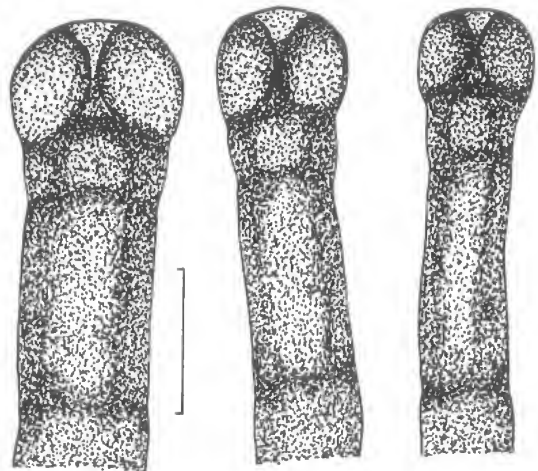


FIG. 5: Dorsal aspect of the distal part of the 4th toe of *Taudactylus diurnus* (left), *T. acutirostris* (middle) and *T. rheophilus* (right).

DESCRIPTION AND VARIATION: Anderson's (1916) and Parker's (1940) definitions are quite sufficient, however the following characters are worth mentioning. This species is a moderate sized taudactylid (males 21.0–26.3 mm (mean 23.66 mm, $N = 39$), females 21.0–27.7 mm (mean 27.19 mm, $N = 17$), in SV length); head narrow, HW/SV ratio 0.301–0.351 and equal in both sexes; disc of digits relatively small, 1.25 width of base of discs. Dorsal skin of body smooth or chagreen and some individuals with distinct short skinfolds on the body, dorsal surfaces of the tibia and posterior surface of the thigh near the cloacal opening. In some individuals the back is marked with inverted V-shaped dark markings, and usually the tubercles which are arranged in a triangle on the lower back are each marked by a black spot. In some individuals the groin is reddish, orange or yellow and in those individuals the proximal surfaces of thigh and ventral surfaces of tibia are also brightly coloured. Generally the throat and anterior portion of the abdomen are cream with dark brown blotches; a round cream spot is present near the base of each forearm, it is very clear when the ventral surfaces of the body are heavily pigmented. Dorsal surfaces of the fore and hind limbs are crossbanded. Mature males with a vocal sac which opens by a slit on each side of the tongue; nuptial pad present, a swollen spinulated pad on the base of the 1st, 2nd and sometimes the 3rd finger; nasals narrow club-shaped bones which are widely separated from each other and not touching the sphenthmoids; fronto-parietal fontanelle narrow, about as wide as the fronto-parietal width at its narrowest portion (Fig. 1B); zygomatic rami of squamosal is 0.3 to 0.5 the length of the otic rami (Fig. 3G); omosternum present; sternum cartilaginous and elongated (Fig. 3C).

TADPOLES: As in *T. diurnus* and *T. eungellensis*, tadpoles have rounded snout in profile and rounded tail tip, spiracle lateral left, and dextral anal opening. Unlike the two species mentioned above, *T. acutirostris* tadpoles are toothed (tooth row formula I, 1/1, I, I($\frac{1}{4}$)), and labial papillae are deeply indented posteriorly and to lesser extent laterally (Fig. 7); the body is broad, BW/BL ratio more than 0.679; the body wall of the posterior portion of the body is transparent and pigmentless, hence the gut is visible from the dorsal, lateral and ventral view. Only the lateral and dorsal side of the head region, the base of the muscular tail, and to a certain extent the tail fins are pigmented. ST length of stages 25–26 are considerably larger in *T. acutirostris* than in *T. diurnus* or *T. eungellensis*, 16.0–36.1 mm for the former against 17.0–30.0 mm for the others; TL/ST and TH/TL ratios are similar for the three species. Unlike any other known Australo-papuan tadpoles, the outer upper labial tooth row lies in alignment with the labial papillae (Fig. 7).

BIOLOGY: Breeding males call during the day as well as during the night from rocks or under roots of shrubs along shady creeks usually with swift running water. Amplexus is inguinal. Breeding was observed in late November through January. Eggs are large 2.2–2.7 mm in diameter and laid as a gelatinous clump of about 25–40 amongst rock in the water usually under heavy shaded places. Tadpoles are bottom dwellers and spend most of the time scraping on rocks or vegetation with their expanded umbrella-shaped lip; the latter also serves for clinging on the substrate. Adults and tadpoles are sympatric and

synchronopatric with *Hyla dayi*, *Hyla spp.*, *Sphenophryne pluvialis*, *Cophixalus ornatus*, *Hyla eucnemis*, *Mixophyes schevilli* in Tinaroo Creek, Kuranda; with *Taudactylus rheophilus*, *Hyla eucnemis*, *H. dayi*, *H. chloris*, and *Mixophyes schevilli* on Mt Lewis; and with *Nyctimystes hosmeri*, *Hyla lesueuri*, *H. dayi*, *H. eucnemis* at Tully's Falls, north Queensland.

CALL: Sharp pitched tapping sound repeated 3–4 times in quick succession. Its loudness is between *T. diurnus* and *T. eungellensis*.

HABITAT: This species is found along small creeks in rain forest (Tully's Falls, Tschooratypa Creek, Palmerston NP, Kuranda, Mt Lewis in N. Queensland) and in wet sclerophyll forest (Tinaroo Creek Road, Jullaten, Speerwah, N. Queensland). These frogs are active during the day, but males were also heard calling at night on Mt Lewis. The vertical distribution ranges from 600 to 1200 m above sea level.

DISTRIBUTION: Along the Great Dividing Range of Queensland. N. Queensland: Mt Lewis, Mt Spurgeon, Jullaten, Kuranda, Speerwah, Malanda, Tinaroo Creek Road, Tully's Falls, Charmillan Creek, 10 km N. Tully's Falls, Tschooratypa Creek–Palmerston NP. Mundubbera, SE. Queensland [?] (Parker, 1940).

REMARKS: Alice Grandison examined the specimen of *Crinia acutirostris* (BM 1938.7.2.I) from Mundubbera, SE. Queensland, which was reported by Parker (1940); although that specimen is in poor condition, she notes (pers comm.) that that specimen ties with *acutirostris* better than with the other three taxa recognized here. Attempts to verify the occurrence of *T. acutirostris* in the Mundubbera area, SE. Queensland, have been unsuccessful.

***Taudactylus rheophilus* sp. nov.**

(Figs. 1A, 2A,C,E, 3A,E, 4C, 5; Plate 29)

HOLOTYPE: Adult female, QM J22418, from Mt Lewis, 1200m above sea level, north Queensland, collected by William Hosmer, 26.xii.1971.

PARATYPES: 2 ♂ (QM J22419–20), 2 ♀ (QM J22426–7), and 2 juveniles (QM J22429–30), type locality, W. Hosmer, 29.iv.1972; 8 ♂ (QM J22421–5, DSL 5964, 5966, 5968); 3 ♀ (QM J22428, DSL 5963, 6324), 2 juveniles (QM J22431–2), type locality, D. S. Liem and W. Hosmer, 27 May 1972; 2 ♀ (DSL 4880, 5975), 12 juveniles (DSL 5482–3, 5933, 5937, 5967, 5972–4, 5976–9), skeleton (DSL 5480), cleared specimen (DSL 5936), type locality.

DIAGNOSIS: This species is distinguishable from the other three species by the following combinations of characters: snout not shovel shaped, dorsal aspect of snout acuminate, vertical in profile and not protruding; head broad, HW/SV ratio 0.365–0.422; ventral surface of body greyish brown with large roundish cream blotches on pectoral region, anterior abdomen, and on flank between base of forearm and groin; mature males with subcutaneous nuptial glands (not spinulated pad) on the base of 1st and 2nd fingers; a narrow greyish inter-orbital streak across the anterior portion of the upper eyelid present; a dorso-lateral irregular light marking runs from behind the eye to the groin; discs of digits small, 1.25 the width of the neck of the disc.

DESCRIPTION OF HOLOTYPE: SV-length 28.5 mm; tibia length 13.5 mm, 0.475 of SV-length; head width 11.5 mm, 0.403 of SV-length; dorsal aspect of snout blunt, acuminate, and vertical in profile (Fig. 4C); EN 1.8 mm; IN 3.4 mm; loreal region sloping; canthus rostralis angular in section, and forming a distinct angle at level of nostrils to converge anteriorly to form an acuminate snout; pupil horizontally oval; tympanum hidden; tongue $1\frac{1}{4}$ as long as wide, widest at $\frac{2}{3}$ its length, straight anteriorly and rounded posteriorly; a distinct pit is present two-thirds down the length of the tongue; posterior two-thirds of tongue free; choanae large and round; vomerine teeth absent; fingers unwebbed, distally expanded into discs; longitudinal groove present on disto-dorsal portion of disc (Fig. 5). Length of fingers from shortest to longest 1-2-4-3; phalangeal formula of hand 2-2-3-3; terminal phalanges of fingers T-shaped; metacarpal tubercle present on all metacarpo-phalangeal joints; subarticular tubercle depressed, that of the 3rd finger usually distinct; lateral palmar tubercle rounded and twice that of oval inner palmar tubercle; toes not webbed, but with distinct toe fringes, width $\frac{1}{3}$ width of toe; distally toes expanded into discs, with longitudinal groove disto-dorsally; length of toes from shortest to longest 1-2-3-5-4; phalangeal formula of foot 2-2-3-4-3; subarticular tubercles ovoid, depressed, formula from 1st to 5th toe 1-2-2-3-2; metatarso-phalangeal tubercle on base of toes ovoid; inner metatarsal tubercle ovoid, outer one absent.

Skin of dorsum smooth, with some small tubercles; skin of throat, chest, abdomen and posterior surfaces of thighs smooth; cloacal opening directed posteriorly at mid-level of thighs.

Dorsal ground colour dark brown with black markings; an irregular greyish streak runs from behind eye to groin and a transverse streak between anterior portion of eyes; loreal region black with some irregular grey markings; lateral surface from behind eyes to half-way to groin jet black; groin region brownish; dorsal surfaces of forelimbs and fingers with dark brown crossbands on light brownish background; medial portion of back of hand immaculate cream; two distinct and one faint cross band on forearm; dark brown cross bands on dorsal surfaces of hind limbs orient obliquely on light brown background; three dark cross bands on femur; two distinct dark brown cross bands on tibia; two vague bands on metatarsal region; toes creamish grey with irregular brown bands; ventral surface of body brownish with bold irregular whitish cream markings; extensive markings extend from between the base of the forearms to halfway down the abdomen, throat with rounded spots on tan background; ventral inner surfaces of humerus and forearms immaculate cream while that of hands and fingers brown; ventral surfaces of the thighs and hind limbs with brownish background with some cream markings on the antero-ventral portion of the thighs and ventral surfaces of the tibia.

DESCRIPTION AND VARIATION: Twelve males 24.3–27.4 mm (mean 26.1 mm) and 9 females 24.1–30.5 mm (mean 28.5 mm) in SV length; HL/SV ratio 0.365–0.421 in males, 0.375–0.412 in females, 0.376–0.422 mm in juveniles ($N = 12$); TL/SV ratio 0.453–0.514 in males, 0.452–0.517 in females, 0.476–0.520 in juveniles; EN/IN ratio 0.563–0.781 in males, 0.579–0.703 in females, 0.522–0.700 in juveniles. Except for the slightly longer SV length in females there is no intersexual variation in the measurements.

Dorsal background colour dark brown to reddish brown, or greyish brown. Dorsal markings vary between individuals in regard to the distinctiveness of the dorso-lateral

irregular marking behind the eyes as well as the interorbital transverse band; some individuals have a marked black irregular hourglass pattern on the back; dorso-lateral light marking sharply meets the dark brown marking on the lateral side of the body, this dark band extends from behind the eyes to the groin; unlike that of the holotype, there is a distinct dark brown streak from below eye to upper jaw, and light cream streaks line both sides; ventral colouration brownish with extensive cream blotches; in some individuals the abdomen appears to be almost completely cream (as in 5939); inner ventral surfaces of humerus and forearm are cream in most specimens examined or yellowish green; ventral surface of fingers with distinct crossbands in some individuals; forearm creamish tan with 2–3 dark crossbands; in some specimens (QM J 22429, J 22420) the dorsal surface of the humerus is almost immaculate cream; dark cross bands on thighs vary from 4 to 6 bands, and are narrower in those with greater numbers; bands on tibia vary from 2 to 3, in some individuals these crossbands are indistinct; 2 crossbands on dorsal surface of foot; dorsal surfaces of fingers and toes are light and dark banded; males without spinulated nuptial pad, but subcutaneous nuptial glands are present on base of 1st and 2nd fingers; males with a vocal sac, and a pair of slit openings on each side of tongue. Colour markings are more pronounced in juveniles. Nasal bones narrow and widely separated from each other and not touching the sphenethmoid; fronto-parietal frontanelle moderately large; zygomatic rami of squamosal as long as that of the otic rami (Fig. 3E), which distinguishes it from the three other species; omosternum present; sternum rounded (Fig. 3A).

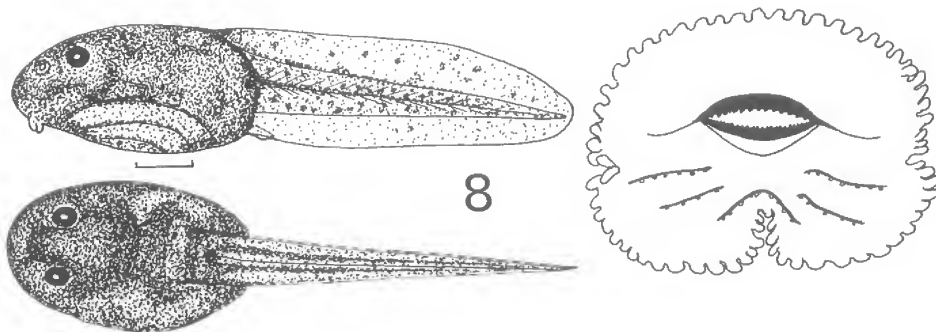
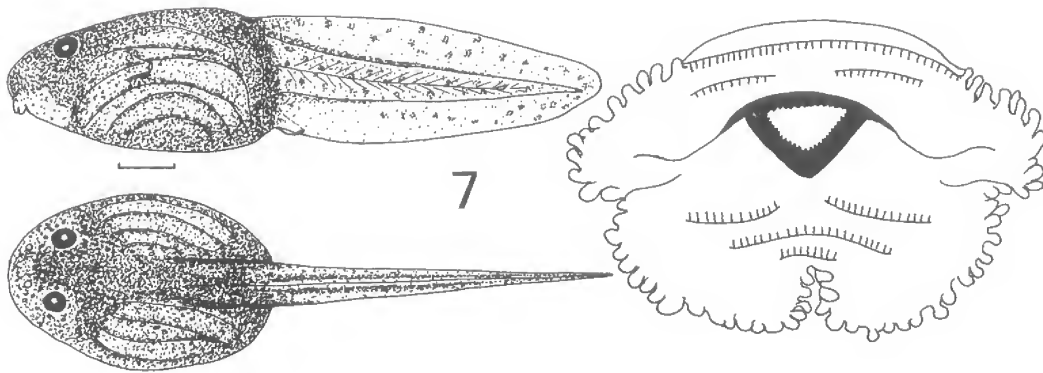
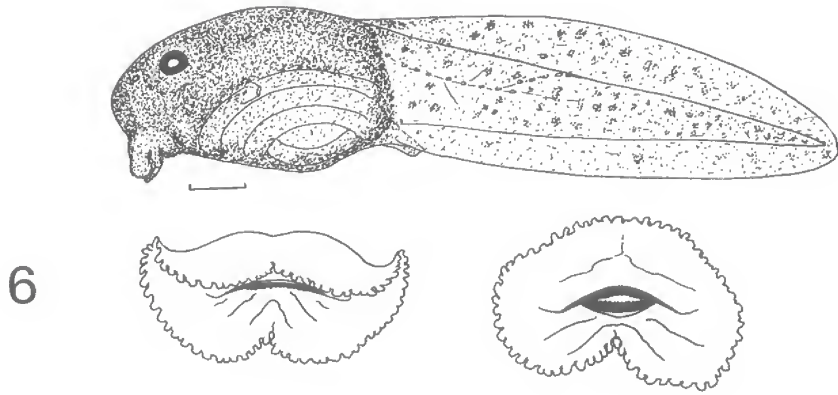
TADPOLES: Egg masses and tadpoles of *Rheophilus* have not been identified. Tadpoles of *Taudactylus acutirostris*, *Hyla eucnemis* and *Mixophyes schevili* were collected in May at the type locality of *Taudactylus rheophilus* on Mt Lewis, N. Queensland, but none could be associated with the new species.

BIOLOGY: Little is known of the life history of this species. This species is very secretive, and was found under rocks and stones under water along swift moving mountain streams, as well as under roots of shrubs. No individuals have been observed sitting on an exposed position as in the three other species. Usually only the eyes and nose stick out of the water amongst rocks. They are active during the day as well as at night. Egg masses and tadpoles of this species have not been identified. Large eggs 1.8–2.4 mm in diameter, numbering 35–50 are found in gravid females. Apparently *T. rheophilus* lays its eggs under rocks in water and the tadpoles probably resemble *T. acutirostris* in having labial teeth and interrupted labial papillae row. Juveniles were collected in December 1971 as well as in May 1972. *T. rheophilus* is synchronopatric with *Myxophyes schevilli*, *Taudactylus acutirostris*, *Hyla eucnemis*, *H. dayi*, *H. chloris*, *Cophixalus fryi*, *C. ornatus*, *Sphenophryne* spp.

FIG. 6: Lateral view of tadpole of *Taudactylus diurnus* at stage 25. Mouth of *T. diurnus* tadpole at rest (left) and open (right).

FIG. 7: Lateral and dorsal aspect of *Taudactylus acutirostris* tadpole; note the extent of transparent body wall. At right, mouth part of *T. acutirostris*; note that the outer labial tooth row lies in alignment with the labial papillae.

FIG. 8: Lateral and dorsal aspect of tadpole of *Taudactylus eungellensis*. At right, mouth part of *T. eungellensis* tadpole; note the ridges and papillae on the lower labium.



CALL: Only one male was heard calling during the day (10.00 a.m.) and this was not recorded. The call is a soft metallic tapping sound repeated 4–5 times in quick succession, the same general pattern as the other three species. The individual was calling between two rocks submerged in water and with only the head above the surface of the water. It paused 2–3 minutes between each call.

HABITAT: This species is found along rocky montane rainforest streams on Mt Lewis, N. Queensland, at an elevation of 1200 m above sea level.

DISTRIBUTION: At present it is only found on the SW. slope of Mt Lewis, N. Queensland.

REMARKS: Unlike the other three species there is only slight sexual difference in regard to the SV length.

ETYMOLOGY: The specific name is derived from the Greek prefix *rheos*, meaning stream, and the Greek word *philos* meaning love or fond of, with reference to the creek-dwelling habit.

DISCUSSION

Species of *Taudactylus* possess some highly adaptive features amongst the Australo-papuan leptodactylids: adults with a distinct digital disc which is grooved longitudinally; T-shaped terminal phalanx; tadpoles toothless with a broad expanded labium surrounded completely by a single row of labial papillae in *T. diurnus* and *T. eungellensis*, while in *T. acutirostris* the tadpoles are toothed, and the row of labial papillae surrounding the expanded labium is interrupted anteriorly. All these known tadpoles possess lateral line organs around the eyes extending posteriorly behind the eyes and branching into two, one leading toward the anal region and another extending along the muscular tail. This structure is apparently only found in this genus amongst the known Australo-papuan leptodactylid tadpoles.

This genus shares numerous features with various myobatrachine members, not only the adult structures, e.g. cricoid does not form a complete ring ventrally, alary process of hyoid apparatus broad and wing-like, M. levator mandibulae subexternus absent, nervus mandibulae lies lateral to M. levator mandibulae externus, etc., but also the tooth row formula in *T. acutirostris* tadpoles resembles most myobatrachine species. Furthermore the tapping call of members of *Taudactylus* resembles *Crinia rosea*. Because *Taudactylus* shares numerous structures with members of Myobatrachinae, it undoubtedly belongs to this group; this concurs with Lynch's (1971, p. 97) conclusion. Amongst the Myobatrachinae, *Taudactylus* appears to be closely related to *Crinia*, sharing the presence of maxillary teeth; absence of outer metatarsal tubercle is shared with *Crinia leai*, *C. rosea*, *C. victoriana*, *C. haswelli*, *C. laevis* and *C. darlingtoni*; small occipital condyles and relatively long zygomatic rami of squamosal are shared with *Crinia* and *Pseudophryne*. The fringed toes of *Taudactylus* are shared with *Crinia haswelli*, *C. riparia*, and *C. sloanei*. Testes of mature *Taudactylus* males are dark brown to black and these are shared with all members of *Kyarranus* and *Crinia*.

In view of the above data it appears that *Taudactylus* most likely was derived from a *Crinia*-like ancestor which had adapted to survive on montane rainforest streams along the Great Dividing Range of eastern Australia.

The early divergence of members of the genus *Taudactylus* is supported by the morphological specialization in adults as well as in tadpoles, the restricted habitat preference in rainforest, and the diurnal habits. *Taudactylus*, with other relict frog species in eastern Australia, occupies disjunct high mountain areas, where relict plant communities e.g. Antarctic beech forest, also occur. Adaptive specialization of relict frogs are expressed in various ways, e.g. terrestrial egg masses and sucker mouth tadpoles in *Mixophyes fasciolatus*, *M. iteratus*, *M. balbus*, and *M. schevilli* (Moore, 1961; Straughan, 1966); development of tadpoles in small pockets of temporary water bodies and tadpole cannibalism in *Lechriodus fletcheri* (Moore, 1961); terrestrial nest and direct development in *Kyarranus loveridgei* (Moore, 1961); and direct development in brood pouches in *Crinia darlingtoni* (Straughan and Main, 1966).

Straughan and Main (1966) discussed briefly the peculiar distribution of New Guinean frogs, where they are restricted to rainforest of north Queensland. Main (1968) has presented a logical explanation of this distribution pattern, and suggested that the northern rainforests which have many New Guinean elements are separated by a wide arid low country from the southern rainforest. Tate (1952) argued that invasion of New Guinean forms appears as a consequence of lower sea level during the pleistocene period, which led to a land mass connecting between North Australia and New Guinea. Straughan and Main (1966) and Main (1968) have suggested that the New Guinean elements had invaded north Queensland recently, probably during the pleistocene, and that they never had crossed the low arid belt between Townsville and Rockhampton. Furthermore they suggested that genera with disjunct north and south rainforest forms (*Mixophyes*, *Lechriodus* and *Taudactylus*) must have spread along the Great Dividing Range prior to the development of the arid belt. Main (1968) added that if the dry belt developed in the pleistocene then *Mixophyes*, *Lechriodus* and *Taudactylus* must have a continuous distribution in the tertiary (probably pliocene). The presence of *Taudactylus eungellensis* in the isolated montane rainforest in Eungella-Finch Hatton area near Mackay, and *T. diurnus* from Kondallilla, SE. Queensland, which were found recently by the senior author, substantiate that at one time this genus had a continuous distribution along the Great Dividing Range.

Taudactylus diurnus is more closely related to *T. eungellensis* than to the two other species sharing numerous derived characters, e.g. broad digital discs, broad toe fingers, absence of omosternum, absence of subarticular tubercles of fingers, absence of vocal sac in males, absence of labial tooth rows and uninterrupted labial papillae in tadpoles. On the other hand *T. acutirostris* and *T. rheophilus* are more closely related to each other than to the two other species, and share some characters which are not shared with *T. diurnus* and *T. eungellensis*, e.g. presence of omosternum, narrow digital discs, narrow toe fringes, presence of subarticular tubercles of fingers, and the presence of a vocal sac in males. *T. acutirostris* tadpoles with labial tooth rows and interrupted labial papillae row are different from those of *T. diurnus* and *T. eungellensis*.

With the exception of the odd occurrence of the questionable *T. acutirostris* from Mundubbera reported by Parker (1940), the divergence of *diurnus-eungellensis* versus *acutirostris-rheophilus* supports the effect of the arid belt which lies somewhere between Rockhampton and Townsville.

Because *T. diurnus* and *T. eungellensis* possess more numerous derived characters than *T. acutirostris* and *T. rheophilus*, it is highly probable the former pair were derived from an *acutirostris-rheophilus* like ancestor. Because *T. eungellensis* tadpoles still possess stronger ridges on lower labium which resemble degenerated labial tooth rows, and because the males have normal loud calls, it is highly probable that this form gives rise to the more specialized *T. diurnus*. The relationship between *T. acutirostris* and *T. rheophilus*, however, is not clear. Finally, one could speculate:

- (1) That either *T. acutirostris* or *T. rheophilus* could be expected in various other isolated mountain rainforest or wet sclerophyll forest along the Great Dividing Range north of Townsville.
- (2) That *T. diurnus* and/or *T. eungellensis* may occur in other montane rainforest or wet sclerophyll forest along the Great Dividing Range between Mackay and Macpherson Range in SE. Queensland.
- (3) That the occurrence of *Taudactylus acutirostris* (*Crinia acutirostris* sensu Parker) in Mundubbera, SE. Queensland (Parker, 1940) is questionable.

Probably *Taudactylus* differentiated from *Crinia*-like ancestors during the Tertiary, about the same period *Crinia darlingtoni* differentiated as suggested by Straughan and Main (1966).

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PLATE 29

Taudactylus rheophilus, QM J22428, Mt Lewis, N. Queensland





A NEW GENUS OF FROG OF THE FAMILY LEPTODACTYLIDAE
FROM SE. QUEENSLAND, AUSTRALIA

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ABSTRACT

A new genus and species of Australo-papuan leptodactylid frog, *Rheobatrachus silus* sp. nov., is described. This genus is monotypic and presently is found only at the type locality, 3 km SW. Montville, SE. Queensland, Australia.

It is the only living leptodactylid having a monocondylar sacro-coccygeal articulation, paired sacral postzygapophyses, and paired coccygeal prezygapophyses. In addition the cricoid is a complete ring, alary processes of the hyoid are broad and wing-like, and the M. petrohyoideus has its anterior insertion along the postero-lateral rim of the hyoid.

This morphological evidence suggests that this genus is one of the most primitive living leptodactylids and can not be placed satisfactorily in either of the two Australo-papuan subfamilies Myobatrachinae and Cyclorantinae *auct.*

During intensive work in Queensland in the past few years, I have collected several new forms of *Hyla*, *Nyctimystes*, *Sphenophryne*, *Taudactylus*, and an undetermined aquatic frog. The latter was collected from a mountain creek in SE. Queensland, Australia, and has a peculiar behaviour.

This new frog differs completely from other Australo-papuan frogs. Externally it resembles the Asiatic ranid, *Ooeidozyga laevis* (Günther), or the Philippine discoglossid, *Barbourula busuangensis* Taylor and Noble, with fully webbed toes, rounded blunt snout, and with prominent eyes close together near the tip; the tongue, which is completely adherent to the mouth floor, resembles *Barbourula busuangensis*; the flattened unwebbed long fingers closely resemble *Xenopus* of Africa.

Observations and drawings were carried out under a Wild stereoscopic microscope. Technique and abbreviations of measurements are described by Liem and Hosmer, 1973.

RELATIONSHIPS AND SYSTEMATIC STATUS

The new taxon differs from other Australo-papuan species or genera currently recognized. Specific and generic status will be considered after the familial allocation for the new taxon has been established.

The new taxon is arciferous, excluding the firmisternous families Ranidae, Rhacophoridae and Microhylidae. Absence of the intercalary cartilage between the two distal

TABLE I
DISTRIBUTION OF CHARACTER STATES IN THE NEW TAXON, MYOBATRACHINAE, CYCLOPORINAE, OTHER LEPTODACTYLIDAE,
MEGOPHYRYINAE, AND OTHER PELOBATIDAE

Numbers in brackets indicate the numbers of genera having a given character state. Lower case letters denote the primitive state, whereas derived states are designated by capital letter with or without an asterisk. Sources of information for 'other Leptodactylidae' are from Trewavas (1933), Griffiths (1963), Dunlap (1960), and Lynch (1971); sources for Megophryinae are from Nicholls (1916), Noble (1922), Trewavas (1933), Liu (1950), Griffiths (1963), Inger (1954, 1966, 1968), Dunlap (1960), Lynch (1971), and personal observations; sources for 'other Pelobatidae' are from Nicholls (1916), Noble (1922), Dunlap (1960), and Griffiths (1963).

	New Taxon	Myobatrachinae (7 genera)	Cyclorantinae (10 genera)	Leptodactylidae (40 genera)	Megophryinae (6 genera)	Other Pelobatidae (4 genera)
1	Vertebral column	A(7)	a(9), A(1)	A(40)	a(2), ?	A(1), A*(1), ?
2	Sacral diapophyses	B(7)	B(10)	B*(32)	b(4), ?	b(4)
3	First two vertebrae	c(7)	C(9), c(1)	c(30), C(8), ?	c(6)	c(4)
4	Cervical cotyles	D*(7)	D(10)	D*(27), D(8), d(2)	d(6)	d(4)
5	Sacro-coccygeal articulation	E(7)	E(10)	E(40)	e(6)	e(1), E(1), E*(2)
6	Postzygapophyses of sacrum	F(7)	F(10)	F(40)	f(1), F(1), ?	f(2), F(1), ?
7	Transverse process of coccyx	G(7)	G(10)	g(1), G(39)	g(1), G(2), ?	g(2), G(1), ?
8	Carpals	h(3), H(2), H*(2)	H(10)	?	?	?
9	Alary process of Hyoid	i(7)	I(10)	i(4), I(30), I*(6)	I*(1), ?	?
10	Cricoid	J(7)	j(10)	J(40)	J(1), ?	J(2), ?
11	Acromion	K(7)	K(10)	K(40)	K(6)	K(4)
12	M. sartorius	L(7)	L(10)	L(40)	L(6)	L(4)
13	M. semitendinosus	M(6), M*(1)	m(6), M*(4)	m(37), M(1), M*(3)	m(6)	m(4)
14	M. adductor longus	N(7)	n(1), N(9)	N(40)	n(3), ?	n(1), N(1), ?
15	M. petrohioideus anterior	o(7)	O(10)	o(3), O(33), ?	O(2), ?	?
16	Orientation of pupil	p(1), P(6)	p(2), P(8)	p(7), P(33)	p(5), P(1)	p(4)
17	Outer metatarsal tubercle	Q(5), q(2)	Q(2), q(8)	Q(36), q(4)	q(3), ?	q(4)
Shared character states*	17-17-0-0	4-3-10-0	3-6-8-0	3-8-5-1	4-6-6-1	6-5-3-3

* The first number denotes the number of states shared with the new taxon, second number denotes the number of states shared with some members of the group, the third number denotes the number of states not in common between the new taxon and a given group, and finally the fourth number denotes the number of states of unknown relationship.

phalanges excludes the Hylidae, Centrolenidae and Pseudidae. Absence of ribs excludes the families Ascaphidae, Pipidae and Discoglossidae. Leptodactylidae and Pelobatidae remain, but the possession of characters distributed randomly between these two make allocation to either difficult.

The new taxon has a monocondylar sacro-coccygeal articulation, sacral postzygapophyses, and coccygeal prezygapophyses—characters not found in Leptodactylidae as currently defined (Lynch, 1971)—and coccygeal transverse processes shared with only *Batrachophrynus* in this group. All of these characters are well represented in some or all members of the Pelobatidae (Nicholls, 1916; Noble, 1922; Griffiths, 1968; Lynch, 1971). In order to get a better picture of relationships, seventeen selected characters are listed in Table 1. Determination of primitive and derived condition is adopted from Marx and Rabb (1970).

Character states are coded as follows:

1. Vertebral column: with intervertebral disc (a), procoelous (A), opisthocelous (A*).
2. Sacral diapophyses: broad (b), moderate (B), narrow (B*).
3. First two vertebrae: free (c), fused (C).
4. Cervical cotyles: large, narrowly separated (d), moderate, moderately separated (D), small, broadly separated (D*).
5. Sacro-coccygeal articulation: monocondylar (e), bicondylar (E), ankylosed (E*).
6. Post-zygapophyses of sacrum or prezygapophyses of coccyx: present (f), absent (F).
7. Transverse process of coccyx: present (g), absent (G).
8. Carpal arrangement: 1st, 2nd, and 3rd carpals free (h), 1st and 2nd free (H), others (H*).
9. Alary process of hyoid: broad, wing-like (i), narrow (I), absent (I*).
10. Cricoid ring: complete (j), incomplete (J).
11. Acromion: absent (k), present (K).
12. M. sartorius: fused to semitendinosus (l), free from semitendinosus (L).
13. M. semitendinosus: distal tendon, ventral to the graciles (m), piercing the graciles (M), dorsal to the graciles (M*).
14. M. adductor longus: partly fused to M. pectineus (n), free from pectineus (N), absent (N*).
15. M. petrohyoideus anterior: inserting on the hyoid plate (o), on the hyoid rim (O).
16. Pupil: vertical (p), horizontal (P).
17. Outer metatarsal tubercle: absent (q), present (Q).

As seen from Table 1, the new taxon shares 4 states with all, 3 states with some members of Myobatrachinae, whereas 10 states are not shared between them; it shares 2 states with all, 6 states with some members and 8 states are not shared with members of Cyclorantinae, etc.

The new taxon shares between 3 to 6 states with all members of other taxa. The new taxon shares 6 states each with some members of Cyclorantinae and Megophryinae, 8

states with other Leptodactylidae, but only 3 states with some members of Myobatrachinae, and 5 states with some members of Pelobatidae. If one adds both categories (sharing with all, and sharing with some members—the first two numbers along bottom row in Table 1), then the new taxon shares 7 states with Myobatrachinae, 9 states with Cyclorhinae, 10 states with Megophryinae, and 11 states each with other Leptodactylidae and other Pelobatidae. However, if one separates the condition of the states (derived or primitive) shared, then it gives a different picture. All states shared between the new taxon with all or some members of Megophryinae (except char. 15) and with all or some members of other Pelobatidae (except char. 1) are primitive. However, on the other hand the new taxon shares two derived states with Myobatrachinae (char. 12 and 14), and three derived states (char. 10, 12, and 15) with all members and 2 derived states (char. 1 and 14) with some members of Cyclorhinae; three derived states (char. 1, 12, and 14) with all, and one derived state (char. 15) with some members of other Leptodactylidae. Derived character states 12 and 14 are shared between the new taxon with all or some members of Leptodactylidae, but not with the Pelobatidae.

Hennig (1965) has argued that primitive condition cannot be evidence of close relationships of their possessors, and only derived states indicate phylogenetic relationships; this concept has been adopted by Tockmorton (1969), Ozeti and Wake (1969), and Liem (1970). Therefore although more numbers of primitive states are shared between the new taxon and Pelobatidae, this does not indicate close relationship. I therefore regard the new taxon as more closely related to the Leptodactylidae, and hence allocate it to that family. However, until more is known about the Megophryinae, possible relationship to this pelobatid may not be discounted. Amongst the leptodactylid genera, only *Batrachophrynus* has fully webbed toes, adherent tongue and transverse process on coccyx (Lynch, 1971) and these are shared with the new taxon. Despite these similarities I do not consider the new taxon closely related to *Batrachophrynus*, because the presence of transverse processes on the coccyx is a primitive condition, and fully webbed toes and adherent tongue which have evolved in other unrelated groups, (e.g. *Barbourula busuangensis* Taylor and Noble), indicate convergence and therefore are not good phylogenetic indicators.

The overall morphology and the geographical proximity suggests that the new taxon is probably more closely related to the Australo-papuan than to the African or New World leptodactylids.

The new taxon is definitely different specifically from any other Australo-papuan leptodactylid frogs; it is the only Australo-papuan species characterized by combinations of the following suite of characters: tongue completely adherent to the mouth floor; toes fully webbed; fingers not webbed; snout short, blunt, rounded; nostril dorsal; eyes close together near the tip of snout; and narrow interorbital space.

Furthermore the new taxon is highly distinctive in other characters (see Table 1), can not be allocated to any Australo-papuan leptodactylid genera, and therefore warrants a generic recognition. Relationship with other genera and subfamilial allocation of the new taxa will be discussed elsewhere (Liem, in MS, 'The Morphology, Systematics and Evolution of the Australo-papuan Leptodactylid and Hylid Frogs.')

Rheobatrachus new genus

TYPE SPECIES: *Rheobatrachus silus*, new species.

DIAGNOSIS: This small frog can be distinguished from other members of Australopapuan leptodactylids by the following combination of characters: (1) pterygoid with a large, ventrally directed lateral flange at the juncture of the three main rami; (2) braincase narrows anteriorly, about half the width at level of fronto-parietal juncture; (3) alary process of hyoid broad, wing-like; (4) sacrum having a monocondylar articulation with coccyx; (5) sacrum has a pair of postzygapophyses which articulate with the prezygapophyses of the coccyx; (6) anterior portion of coccyx with a pair of short triangular transverse processes; (7) first and second vertebrae free; (8) cotylar surfaces large, and close to each other; (9) omohyoideus absent; (10) petrohyoideus anterior inserts on the hyoid rim; (11) feet fully webbed; (12) fingers free; (13) hind limbs robust; (14) eyes large, close together; (15) snout short, pugnose; (16) tongue completely adherent to the mouth floor.

CONTENT: Monotypic genus: *Rheobatrachus silus*, new species.

DESCRIPTION: Snout short, rounded, pugnose; loreal region round; nostrils dorsal; pupil rhomboidal when constricted; eyes dorsal, close together; tongue oval, and completely adherent to the mouth floor; choanae moderate, rounded; vomerine teeth absent; vocal sac present, with a pair of slit-like openings. Fingers unwebbed, slightly flattened, tapering off distally; formula of the hand 2-2-3-3; first finger as long as second; toes fully webbed; distal digits expanded into a disc without a longitudinal or ventro-marginal groove; foot formula 2-2-3-4-3; hind limbs are robust.

OSTEOLOGY: Premaxillary with a small medial and large lateral alae, and inclined dorsally; maxillary and premaxillary teeth are 'fang-like' (Fig. 1E); quadratojugal present, widely overlapping with the maxilla.

Vomerine teeth absent; vomerine bone sickle-shaped on medial sides of choanae; palatine bone moderate in size and curved; parasphenoid dagger-shaped and does not reach the level of the palatine; medial arm of pterygoid not touching the lateral ala of parasphenoid. Septomaxilla present; nasal club-shaped, narrowly separated from each other but not touching the sphenethmoid, and is in tenuous contact with the palatine; sphenethmoid entire, deeply indented longitudinally at the postero-dorsal portion (Fig. 1C).

Fronto-parietal narrows anteriorly, to embrace the sphenethmoid; fronto-parietal fontanelle relatively large; carotid canal or shallow carotid channel absent; orbital fenestra is large for a leptodactylid.

Squamosal moderate in size; otic ramus narrow and half the length of zygomatic ramus; pterygoid moderate in size, the anterior arm is moderately separated from palatine; pterygoid has a large ventrally directed flange at the juncture of the three arms (Fig. 1D); columella cylindrical; occipital condyles are extremely large, and narrowly separated from each other; prootic and exoccipital are not completely fused; jugular foramen, prootic are evident.

There are eight presacral vertebrae; the first three are wider than the posterior ones; cervical and 2nd vertebrae are free (Fig. 2A); cervical cotyles large, in tenuous contact mid-ventrally (Fig. 2C); the sacral diapophyses are greatly expanded (Fig. 2A and D); sacral vertebra articulates with a single condyle to the coccyx (Fig. 2F); sacrum has postzygapophyses (Fig. 2D) which articulate with the prezygapophyses of the coccyx; coccyx with a pair of short triangular transverse processes (Fig. 2A and F).

Pectoral girdle arciferous; left epicoracoid lies ventral to the right one; epicoracoid horns present; epicoracoid intersleeves in the cartilagenous rounded sternum; omosternum present but fused with epicoracoid plate; clavicle narrow, curved; coracoid stout and straight but makes an angle with the longitudinal axis (Fig. 3E); acromion absent (Fig. 2B), this condition differs from any other *Australo-papuan leptodactylids*.

Ilium rounded in cross section; dorsal crest of ilium absent; dorsal protuberance moderately large; there is no dorsal acetabular expansion of the ilium.

Terminal phalanx is broadly knobbed distally (Fig. 2E); fingers and toes relatively long; radiale, ulnare, naviculare, 1st, 2nd and 3rd carpales are free, whereas 4th and 5th carpales and the post-axial centrale are fused (Fig. 1A); prehallux consists of two segments and articulates on 1st carpal; naviculare is in contact with the radiale.

Naviculare and 1st tarsale are free, whereas the 2nd, 3rd and 4th tarsale are fused, the prehallux is simple, consisting of two segments which attach to the naviculare (Fig. 1B).

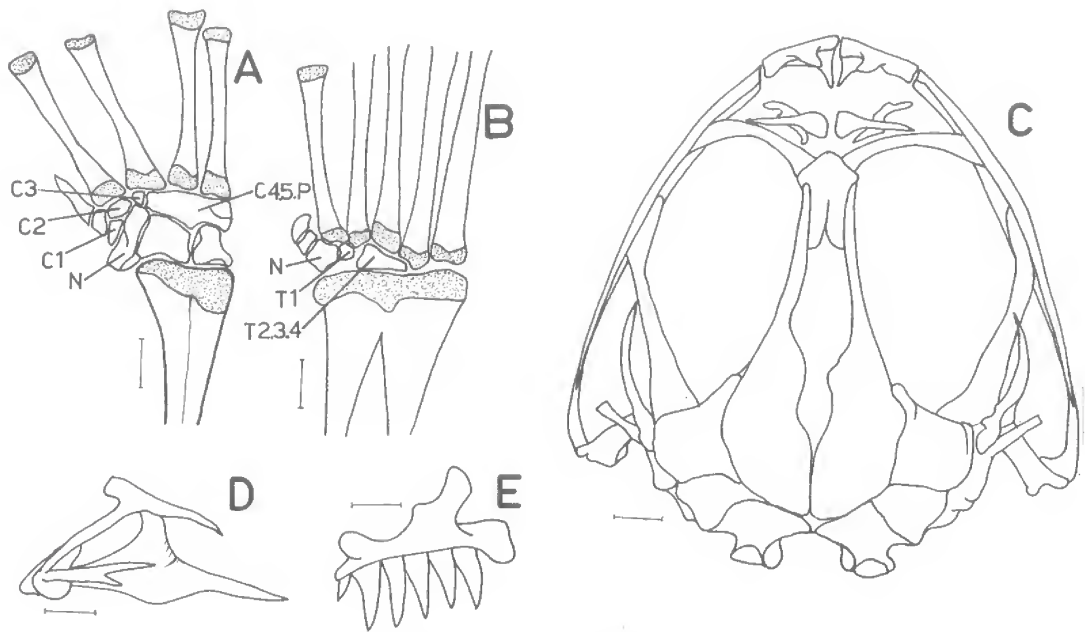


FIG. 1: A, Dorsal view of carpal region of right hand; B, Dorsal view of tarsal region of right foot; C, Dorsal view of skull; D, Lateral view of pterygoid, squamosal, and quadratojugal; E, Anterior view of premaxilla. Lines equal 1 mm.

C1, 1st carpal; C2, 2nd carpal; C3, 3rd carpal; C4.5.P, fusion of 4th, 5th carpal and postaxial carpal; N, naviculare; T1, 1st tarsal; T2.3.4, fusion of 2nd, 3rd and 4th tarsal.

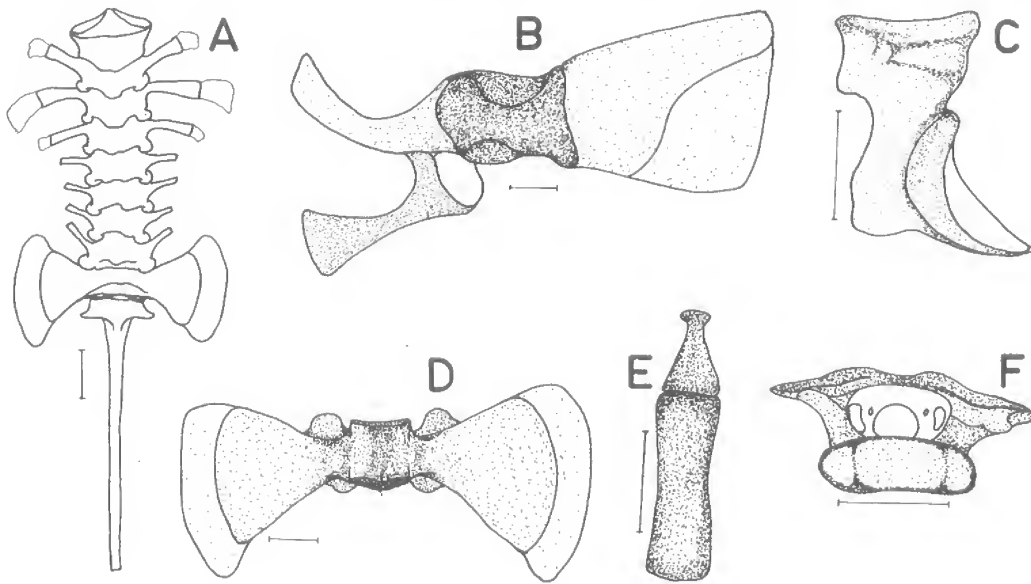


FIG. 2: A, Dorsal view of vertebral column; B, External view of scapular region, note absence of acromion; C, Lateral view of cervical vertebra; D, Ventral view of a sacral vertebra, note presence of postzygapophyses; E, Dorsal view of two distal phalanges of 4th toe; F, Anterior view of coccyx, note presence of prezygapophyses and single articular condyle. Lines equal 1 mm.

Alary processes of the hyoid are broad, wing-like (Fig. 3A); posterior lateral processes are relatively large; thyrohyal large; hyale with a knobbed anterior cornu. Cricoid ring complete, with one medio-dorsal, and two lateral ventral pointed processes (Fig. 3C); muscular processes obvious; larynx without frenulum chordae vocalis; apex of glottis opening orients anteriorly, and differs from any other Australo-papuan leptodactylids.

MYOLOGY: Nervus mandibulae lies lateral to *M. levator mandibulae externus* and *subexternus* (Fig. 3B). Depressor mandibulae consist of one large fan-shaped muscle inserting on otic ramus of squamosal and suprascapular region; *M. submaxillaris* without an apical element; *M. supracoracoideus profundus* is distinct from *superficialis*, but lies dorsal to distal tendon of *M. coracoradialis*; *M. humerodorsalis* consists of one muscle which distally inserts on distal portion of the metacarpal of 2nd, 3rd and 4th finger; *M. supinator manus* consists of two slips, one originating from disto-lateral portion of humerus, the other from disto-lateral portion of the radio-ulna; palmaris complex is a terrestrial type, one *M. palmaris longus* attaches to the aponeurosis palmaris, and the *tendo superficiales* in turn originate from this aponeurosis; *M. adductor longus* is present inserting directly on disto-ventral portion of femur; distal tendon of *M. semitendinosus* lies ventral to distal tendon of the graciles muscles; accessory slip of *M. adductor magnus* absent; *M. extensor cruris brevis long*, inserts along distal three fourth of cruris, and is medial to *M. tibialis anticus brevis*; *M. tibialis anticus brevis* moderate in size; *M. extensor digitorum communis longus* present, and distal tendon inserting on

disto-dorsal portion of metatarsals of 3rd, 4th and 5th toe; plantaris complex is a terrestrial type: distally aponeurosis plantaris inserts on disto-ventral aspect of the fibulare, on medio-ventral portion of distal tendon of *M. flexor digitorum brevis superficialis* at which point it gives rise to a slender tendon which contributes to the formation of the 3rd tendo superficialis; *M. abductor brevis plantaris hallucis* and its accessory slips are absent; *M. abductor prae hallucis* short; only one slip of *M. lumbricalis longus* is present on 2nd toe. *M. extensor brevis superficialis* of 5th toe absent; *M. extensor brevis medii* inserting on 1st, 2nd and 3rd toe; *M. omohyoideus* absent; *M. geniohyoideus* is one continuous muscle straddling the *M. sternohyoideus*, the slip which lies medial to the sternohyoideus inserts on the proximo-medial portion of the thyrohyal and the other slip which lies lateral to the sternohyoideus inserts on the distal portion of posterior lateral process; *M. sternohyoideus* consists of one muscle inserting on the base of the broad wing-like alary process of the hyoid plate; *M. petrohyoideus anterior* inserts on the postero-lateral rim of the broad alary process; *M. petrohyoideus posterior* consists of two slips (Fig. 3A); *M. dilator laryngis* consists of one slip; *M. constrictor anterior* inserting on the raphe of the *M. constrictor externus* (Fig. 3D).

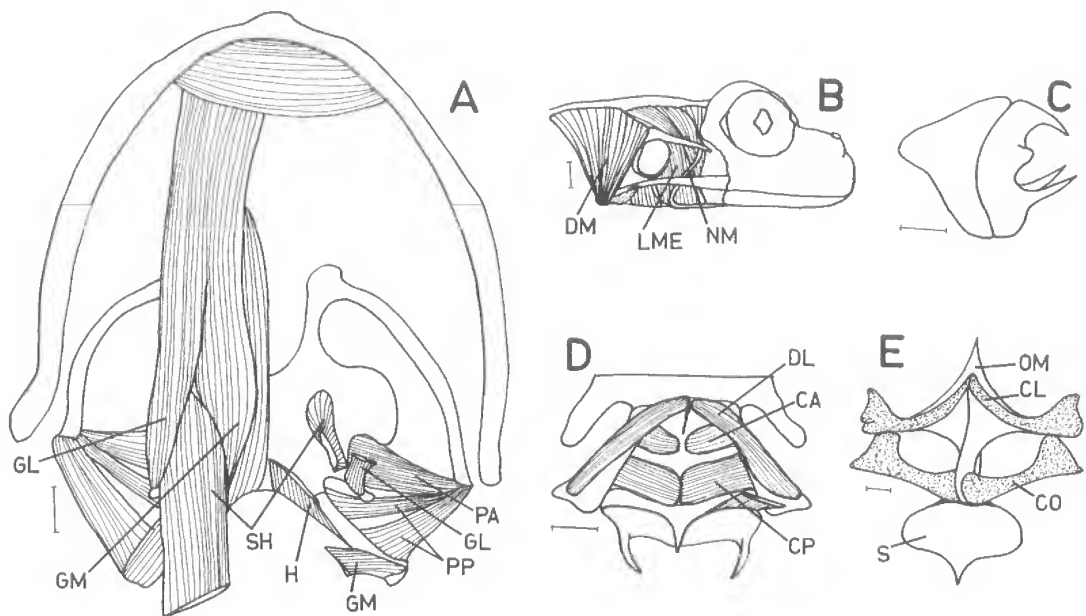


FIG. 3: A, Ventral view of hyoid region; B, Lateral view of head musculature; C, Lateral view of cricoid and arytenoid; D, Dorsal view of laryngeal region; E, Ventral view of pectoral region. Lines equal 1 mm. CA, *M. constrictor anterior*; CL, clavicle; CO, coracoid; CP, *M. constrictor posterior*; DL, *M. dilator laryngis*; DM, *M. depressor mandibulae*; GL, *M. geniohyoideus lateralis*; GM, *M. geniohyoideus medialis*; H, *M. hyglossus*; LME, *M. levator mandibulae externus*; NM, *nervus mandibulae*; OM, *omosternum*; PA, *M. petrohyoideus anterior*; PP, *M. petrohyoideus posterior*; S, *sternum*; SH, *M. sternohyoideus*.

MISCELLANEOUS STRUCTURES: The pupil is rhomboidal, orients vertically; ventral surfaces of body smooth; tongue completely adherent to the mouth floor; nipple-like glands on base of forearms absent; inner metatarsal tubercle present, oval; outer metatarsal tubercle absent; males with subgular vocal sac, with a pair of slit openings; males with spinulated nuptial pads on the medio-dorsal surfaces of the first finger. Egg masses and tadpoles are unknown.

***Rheobatrachus silus* sp. nov.**

HOLOTYPE: Adult male, Queensland Museum J22489, from Kondalilla, 3 km SW. Montville, SE. Queensland, Australia, 500 m above sea level, collected by David S. Liem on 2 June, 1972.

PARATYPES: Four males (QM J22490–93) collected on 30 June 1972, two males (DSL 6332, DSL 6322) collected on 2 June 1972, two females (QM J22494–95) collected on 30 June 1972, two juveniles (QM J22496) collected on 2 June 1972, one juvenile (QM J22497) collected on 17 May 1972; all specimens collected from the type locality by David S. Liem. One dry skeleton (DSL 6320) prepared from a specimen from the type locality by David S. Liem.

DIAGNOSIS: This species is distinguishable from any other living Australian frogs by the following combination of characters: tongue completely adherent to the mouth floor; toes fully webbed reaching the toe disc; fingers free of web, 2nd finger slightly shorter, and 3rd finger slightly longer than the others; distal segment of fingers and toes expanded into rounded disc, without a circum-marginal, ventromarginal or a longitudinal groove; intercalary cartilage absent; pectoral girdle arciferous; inner and outer metacarpal tubercles depressed; interorbital space narrower than the width of the upper eyelid; eyes dorsal and located close to each other; nostrils orient dorsally; hind limbs robust.

DESCRIPTION OF HOLOTYPE: SV length 38.4 mm, tibia length 16.5 mm, 0.427 of SV length; head width 12.3 mm, 0.320 of SV length; snout short, dorsal aspect rounded; EN 2.1 mm; IN is 2.6 mm; interorbital width 1.9 mm; width of eyelid 2.7 mm; snout length 4.3 mm; EN/IN is 0.898; EN/SL 0.487; IO/EW is 0.650. Loreal region sloping; canthus rostralis rounded in section; nostrils dorsal, close to each other, with a distinct rounded tubercle on the posterior rim; pupil vertical, rhomboidal; tympanum hidden under the skin; tongue papillose, completely adherent to the mouth floor, 1.2 as long as wide, widest at 2/3 down its length, with a distinct fissure along its postero-medial half; vocal sac present with a pair of round vocal sac openings on the mouth floor, on each side of the tongue. Fingers unwebbed, distally expanded into rounded discs, with no circum-marginal nor longitudinal groove present on the disc; 2nd slightly shorter, 3rd slightly longer than the other fingers; length of fingers from shortest to longest 2-1-4-3; phalangeal formula of hand 2-2-3-3; a large nuptial pad present on dorso-medial surface of 1st finger from base to almost the distal phalanx, with dark brown to black conical spinules; ventral surfaces of fingers and finger discs finely spinulated; subarticular tubercles absent; metacarpal tubercles present between metacarpo-phalangeal joint of all fingers; inner palmar tubercle is elongated on base of thumb, the outer one is roundish on proximo-lateral portion of palm; both palmar tubercles are flattened, heavily spinulated; distally the toes are expanded into rounded discs, without circummarginal nor longitudinal

groove; toe discs larger than finger discs; toes fully webbed, web reaching base of toe discs. A dermal fringe is present along the medial edge of 1st toe; length of toes from shortest to longest 1-2-3-5-4; phalangeal formula of foot 2-2-3-4-3; two outer metatarsals of toes are not separated by a web; only the proximal subarticular tubercle of 3rd, 4th and 5th toe is present, and is finely spinulated; metatarso-phalangeal tubercle of the 1st, 2nd, 3rd and 5th toe are round, that of 4th toe absent; inner metatarsal tubercle elongated and finely spinulated, whereas the outer one is absent; posterior surfaces of tarsal region heavily tubercular tipped with cream spinules. Cloacal opening is directed posteriorly high between the thighs.

Skin of dorsum chagreen, with numerous tubercles of various sizes; upper eyelid heavily tubercular; ventral surfaces of throat, chest, abdomen and limbs smooth; skin of ventral surfaces of the body are heavily invested with subcutaneous glands, and they could clearly be seen through the skin. Pores of these subcutaneous glands are visible on the dorsal surface of the body; a supra-anal transverse skinfold is present above the cloacal opening.

Dorsal ground colour brown to brownish olive, with round dark blotches on the back; a dark brown streak runs from behind the eye toward the base of the forelimbs; left forearm with two, and right forearm with three cross bands; fingers with light and dark brown markings; dorsal surface of thigh vaguely crossbanded; dorsal surface of tibia with three cross bands; three outer toes crossbanded dorsally; ventral surface of throat, chest and abdomen cream; ventral surfaces of humerus, femur, tibia and tarsus are bright orange (disappears in preservative); ventral surfaces of the hands and feet are greyish black, as are the posterior surfaces of the thighs; pupil is surrounded by a golden rim, eye black with gold spots.

DESCRIPTION AND VARIATION: Paratypes of six males, two females and three juveniles all from the type locality. Males ranging 36.5–40.2 mm (median 38.6 mm) in SV length. HW/SV 0.330–0.357; EN/IN 0.750–0.880; EN/SL 0.488–0.558; IO/EW 0.633–0.731. Adult females 38.1 and 38.9 mm in SV length; TL/SV 0.429–0.454; HW/SV 0.347–0.354; EN/IN 0.821–0.852; EN/SL 0.523–0.535; IO/EW 0.724–0.759. There are no marked intersexual or intrasexual variations in measurements and ratios compared with those of the holotype. One male (QM J22490) is larger than the two females. Ratios of measurements of juveniles fall within the ranges of adults.

In preservatives, the dorsal ground colour of *Rheobatrachus silus* varies from brownish olive to uniform jet black; three males (QM J22491–93), two females (QM J22494–95) and one juvenile (QM J22497) are uniformly black, hence the dorsal dark markings are indistinct. The remaining paratypes and the holotype are light, brownish olive ground colour with rounded or irregular dark markings and cross bands on limbs. There are dark patches at angles of the throat in the dark variant. In life the dorsal colour varies from brownish olive to jet black; colour can change from light brown olive to jet black in live individuals.

HABITAT: This species is found along rocky mountain streams in wet sclerophyll forest in Kondalilla, 3 km SW. Montville, SE. Queensland, Australia, at an elevation of 450 m above sea level.

BEHAVIOUR: *Rheobatrachus silus* is nocturnal, habitually sitting on or clinging half-way submerged to rocks in water. By day it hides submerged under rocks and has not been observed to breathe. Submerged specimens have been kept under observation for over three hours but the total time under water is not known; after prolonged submergence it surfaces slowly and clings to a rock with the head just breaking the surface. The initial inhalation is vigorous accompanied by a growling sound and a disturbance of the immediate surrounding water; subsequent breathing is normal. When disturbed, *Rheobatrachus silus* jumps unpredictably, dives into water exhaling air, presumably to reduce bouyancy, and hides on the bottom or under rocks.

The ability of *Rheobatrachus silus* to swim forward and backward is unusual; the movement of all four limbs suggests crawling through water and is also observed in *Pseudophryne*, amongst Australo-papuan frogs, but is atypical of frogs.

Feeding has not been observed, though moths, Diptera, and Neuroptera placed in the aquarium disappear overnight. Small fish are not touched. No call has been associated with *Rheobatrachus silus*.

REMARKS: The life history is unknown. Two specimens (male and female) collected in June showed undeveloped ovaries, with unpigmented eggs, a straight fallopian tube, and large fat bodies in female; in the male, round cream testes spotted with black pigments and large fat bodies. The condition of nuptial pads and gonads and the presence of large juveniles in May and June suggests that this species is a summer breeder. Gut content of two specimens examined contained insect remains and sand, but no plant materials. Adipose tissue is extensively distributed under the skin, e.g. on the angles of the jaw, corner of M. hyoglossus, groin region, along the sacral region, and between tympanic region and base of forearm. Subcutaneous glands are uniformly distributed throughout the body, and probably this is the main reason why these frogs are very slippery when handled.

Rheobatrachus silus is synchronopatric with *Taudactylus diurnus*, *Hyla leseueri*, *H. glauerti*, *H. pearsoniana*, *Adelotus brevis* and *Mixophyes fasciolatus*.

DISTRIBUTION: At present it is only found from the type locality; recently Glen Ingram (pers. comm.) informed me that it is also found 15 km SW from the type locality.

ETYMOLOGY: The specific name is derived from Latin '*silus*', meaning '*pug nose*', which refers to the blunt snout.

DISCUSSION

The habitus of *Rheobatrachus silus* together with the unique free fingers, broadly webbed toes, and adherent tongue are undoubtedly adaptive specializations to aquatic life; similar modifications also occur in *Barbourula busuangensis* Taylor and Noble.

The presence of sacral postzygapophyses, coccygeal prezygapophyses, transverse processes on coccyx and monocondylar sacro-coccygeal articulation suggest that *Rheobatrachus* is probably one of the most primitive living leptodactylid frogs. The restricted distribution of this genus on the Great Dividing Range suggests that *Rheobatrachus*, together with *Mixophyes*, *Lechriodus*, *Crinia darlingtoni*, and *Taudactylus diurnus* are relict forms which survived along the SE. Queensland refuge belt.

ACKNOWLEDGEMENT

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PLATE 30

Holotype of *Rheobatrachus silus*, male. (QM J22489). Photographed by Owen Kelly.





A REVIEW OF *CLETODES* (CRUSTACEA: HARPACTICOIDA), WITH
THE DESCRIPTION OF A NEW SPECIES FROM QUEENSLAND

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C.S.I.R.O., Cronulla, N.S.W.*

ABSTRACT

Cletodes millerorum sp. nov. is described and figured from a single female associated with a hermit crab, *Dardanus megistos* (Herbst), between tide-marks at Green Island, near Cairns (North Queensland). It is shown that in those species of *Cletodes* in which both sexes are adequately known, the nature of the endopod of P3 in the male is fully correlated with the setation of this ramus (and partly correlated with that of certain other rami) in the homospecific female; on this basis, the above species of *Cletodes* fall into three groups. Assuming that these correlations hold good for poorly known species, the undiscovered male of *C. millerorum* probably has an unmodified third endopod.

The possible taxonomic values of the somitic and opercular sensillae, the opercular teeth, the rami of the maxillule, and the 'membranous tubes', are discussed; all these features are difficult to see and have therefore been largely ignored in the past, but would repay careful study in all species.

It has been found impracticable to contain all the species now known in a single key covering both sexes, as hitherto; separate keys to each sex are therefore provided.

Since the last key to *Cletodes* (Lang, 1965, p. 426), the number of known species has almost doubled; the additions are *C. reyssi* Soyer, 1964, *C. latirostris* Drzycimski, 1967, *C. spinulipes* Por, 1967, *C. yotabis* Por, 1967, *C. smirnovi* Bodin, 1970, and *C. pseudodis-similis* Coull, 1971. A further species (Krishnaswamy, 1957, p. 78, as *Enhydrosoma* sp.) was referred to *Cletodes* by Lang (1965, p. 431) but omitted from his key, probably because of insufficient descriptions and figures (cf. Lang, 1965, p. 7); not having been able to consult Krishnaswamy's paper, I have had to leave out this species altogether.

The discovery of yet another species, the first *Cletodes* to be reported from Australian waters, affords a convenient pretext for taking stock of certain characters which may throw light on relationships within this genus.

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MATERIAL AND METHODS

Among the washings of a gastropod shell tenanted by the pagurid *Dardanus megistos* (Herbst), collected by me at low tide on 20.vii.1970 about 400 m north of the main landing-jetty on Green Island (off Cairns, Queensland), were the following organisms:

KINORHYNCHA

1 echinoderid sp.

MYSIDACEA

A few of ?*Heteromysis* sp.

DECAPODA

1 *Aretopsis* sp. (Alpheidae)

HARPACTICOIDA

6, 3, 7, 4, *Paraidya major* Sewell (i.e. 6 females of which 3 were ovigerous, 7 males, and 4 copepodites); 6, 5, 6, 0, *Porcellidium* (?*ovatum* Haller); 2, 0, 0, 0, *Dactylopodia tisboides* (Claus); 1, 0, 0, 0, *Robertsonia barnesi* Hamond (in press); and 1, 0, 0, 0, *Cletodes millerorum*, described below. Apart from the holotypes of the two new species, all harpacticoids are being retained in my own collection for comparison with material to be studied in future.

The copepods were studied by my usual methods (Hamond, 1969 and in press).

***Cletodes millerorum* sp.nov.**

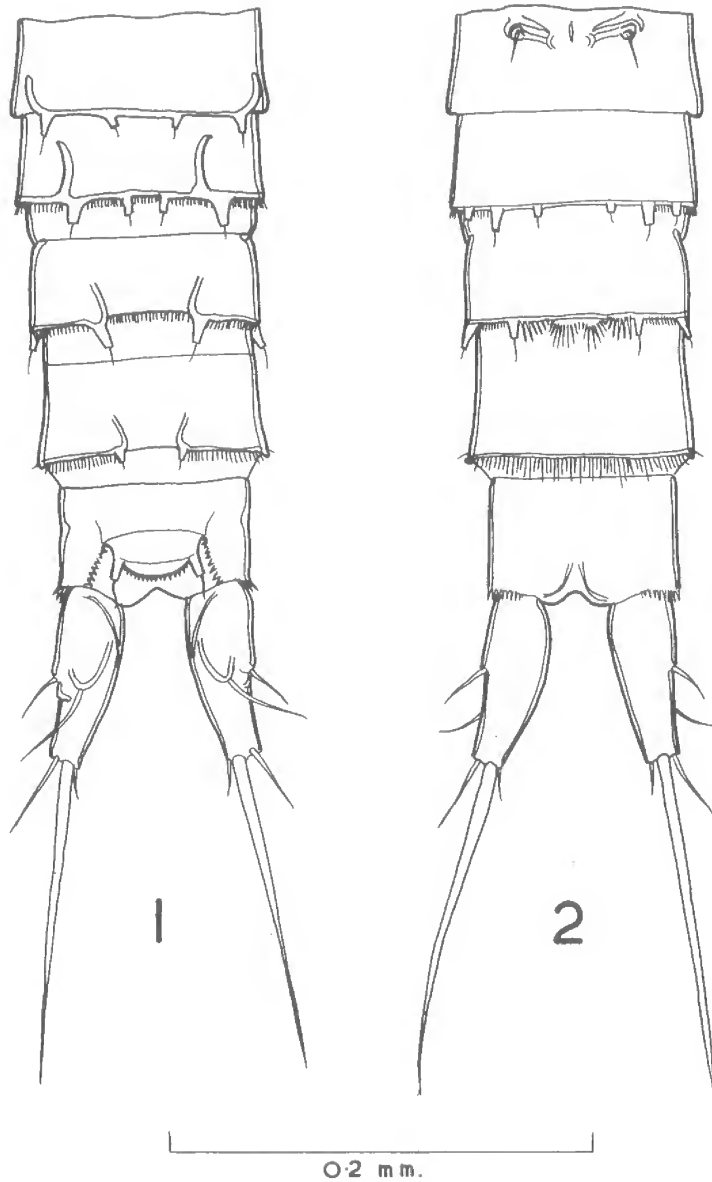
(Figs. 1–14)

HOLOTYPE: Female (apparently adult but not ovigerous), W3811 (Queensland Museum).

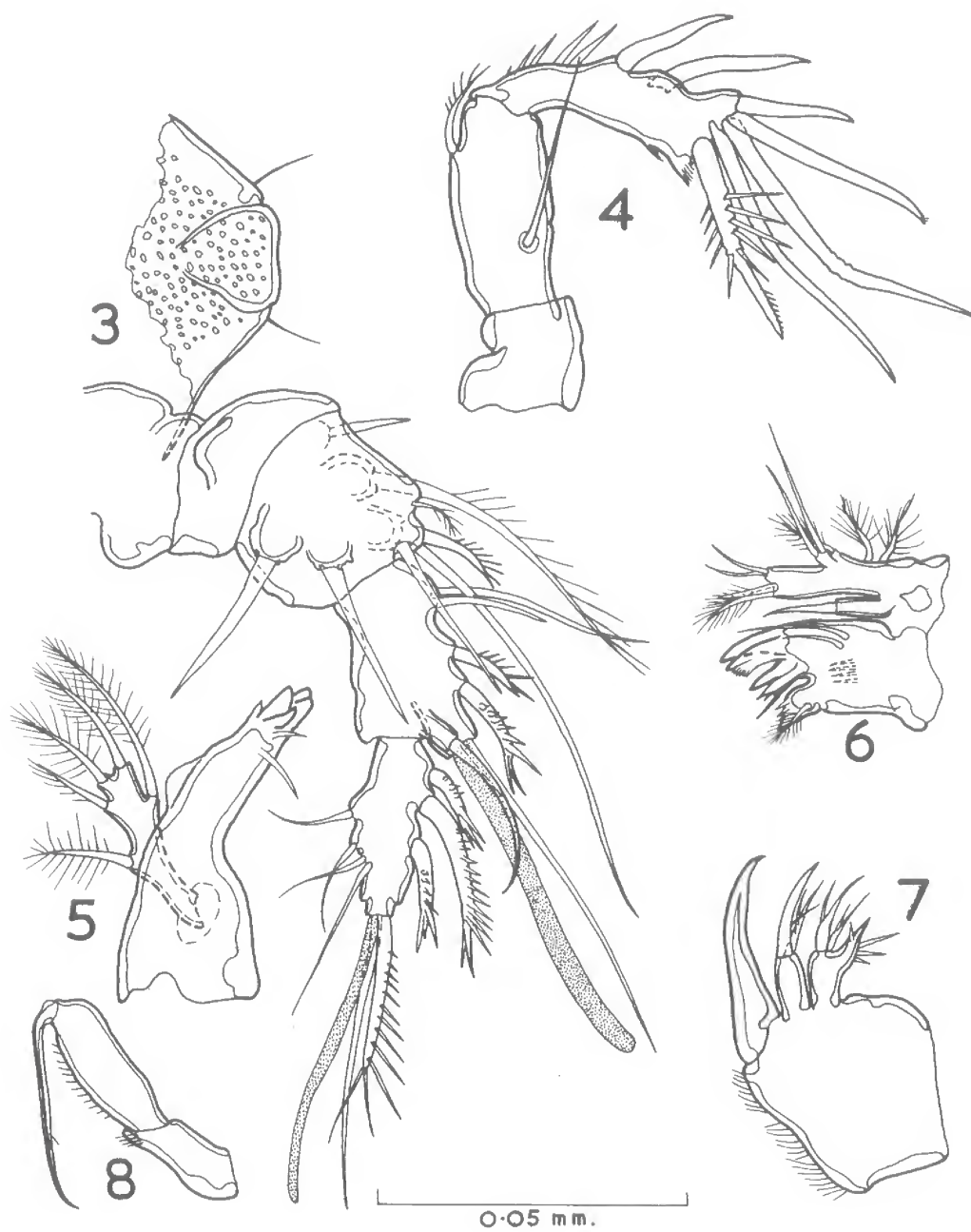
DESCRIPTION: Body 0.6 mm long, slender and tapering towards the furca. Rostrum (Fig. 3) short and blunt; abdomen (reconstructed in Figs. 1 and 2 from a squashed preparation) with the rear edge of each somite bearing combs of very small spinules interrupted by prominent sensillae. Genital double-somite divided distinctly on the dorsal side but much less clearly so on the ventral side. Operculum curved, with a sensilla at each end, and with sixteen very small triangular teeth inserted into an otherwise smooth edge. Furcal rami slightly divergent, separated at their bases by about the width of a ramus; each ramus is about three times as long as its greatest width, which is about one-quarter of the ramal length from the base, and curves slightly outwards. The ramus bears three terminal setae (of which the middle one is by far the largest), a dorsal seta arising from a protuberance, and a lateral seta arising from a step in the external wall.

Antennule (Fig. 3) with the small penultimate segment apparently fused with that proximal to it (i.e. the segment bearing the larger aesthetasc); on the other hand, the proximal part of the antennule appears to be divided into three segments, as shown, instead of the usual two segments, so that the whole antennule consists of five segments as in other *Cletodes* spp., although these segments are not morphologically equivalent to the segments in the latter. This may be an abnormality; however, it is identical in both antennules of the present specimen.

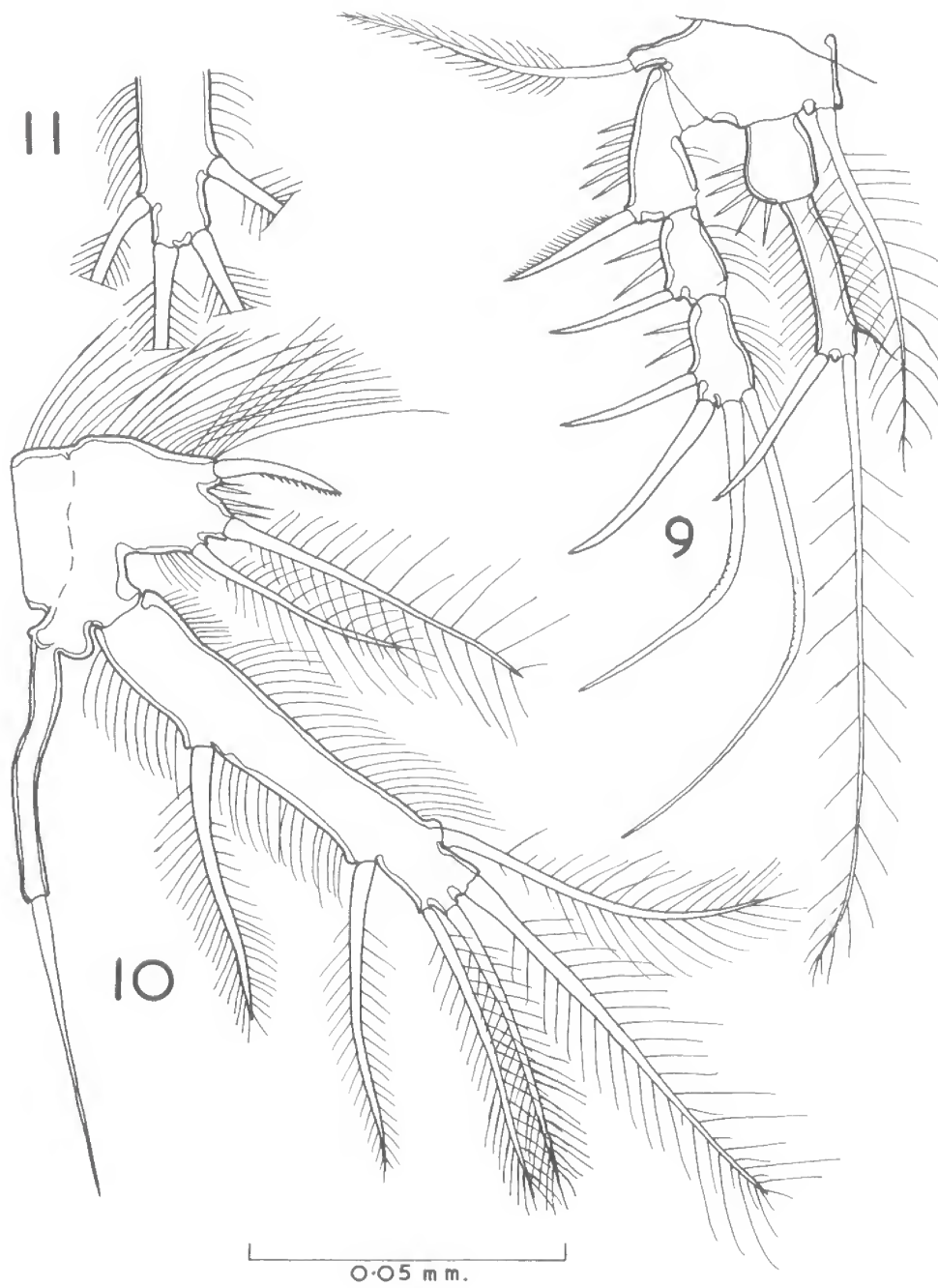
Antenna (Fig. 4) with the exopod represented only by a seta; mandible (Fig. 5) with a single-segmented exopod bearing five plumose setae; maxillule (Fig. 6) like that of *C. hartmanae* Lang, 1965, but with a much more elaborate cutting edge; maxilla (Fig. 7) with two endites; maxillipede (Fig. 8) with a very slender claw, and with a comb of setules along the palmar surface, but without any setae.



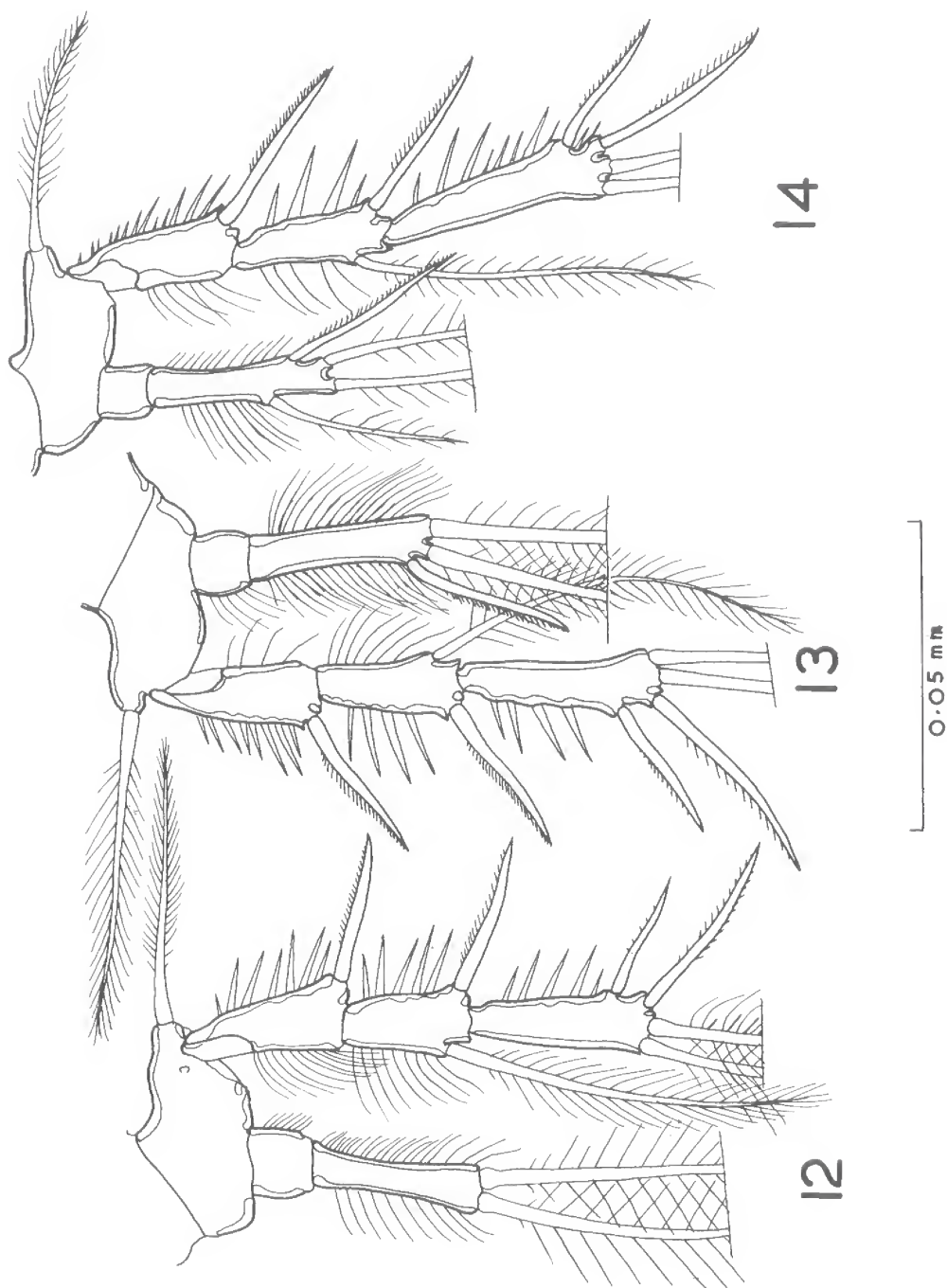
FIGS. 1, 2: *C. millerorum*, abdomen. 1, dorsal view; 2, ventral view.



FIGS. 3-8: *C. millerorum*. 3, rostrum with antennule; 4, antenna; 5, mandible; 6, maxillule; 7, maxilla; 8, maxillipede.



FIGS. 9–11: *C. millerorum*. 9, P1; 10, P5; 11, apex of other exopod of P5.



FIGS. 12-14: *C. millerorum*. 12, P2; 13, P3; 14, P4.

Swimming-legs each with the three-segmented exopod longer than the two-segmented endopod; in P1 (Fig. 9) the second endopod segment is the only one to have an inner seta. Setal formula is P2 (Fig. 12) exp 0.1.022, enp 0.020; P3 (Fig. 13) exp 0.1.022, enp 0.021; P4 (Fig. 14) exp 0.1.022, enp 0.121. P5 with discrete rami; one exopod has six setae (Fig. 10), the other only five (apex in Fig. 11). The two basiendopods are exactly alike, each with three setae, of which the innermost is spiniform with spinules confined to its outer (concave) edge.

Colour in life unknown; in formalin-sea water greyish white. Male hitherto unknown.

I have much pleasure in naming this species after Mr and Mrs Miller, the owners of the Green Island Aquarium in 1970, thanks to whose hospitality I was able to collect this and other harpacticoids on the shores of Green Island.

DISCUSSION

Using the keys by Lang (1948) and by Soyer (1964), *C. millerorum* comes nearest to *C. limicola* or *C. carthaginiensis*; Lang's later key (1965) brings it to *C. dissimilis*. From all these species, however, *C. millerorum* differs either in the form and setation of the female P5 or in the form of the furca. Attempts to make a new key covering both sexes were unsuccessful; separate keys to males and females are given below.

Further details about previously known species of *Cletodes* are given by Klie (1950), Soyer (1964), Bodin (1964a, 1970), and Por (1959, 1964); the taxonomically awkward variability of the furca, in material identified by Por (1964a) as *limicola*, is supposed by Bodin (1970) to be due to confusion with *C. spinulipes* or a similar species. Since *C. limicola* may have a small spine on the basiendopod in addition to the usual setae (Soyer, 1964, fig. 1E; Bodin, 1970, however, describes this as a membraneous tube), I can find no reason at present to maintain the var. *tunisensis* Monard, especially in view of the low standard of Monard's descriptions and figures and the fact (for which I am indebted to Professor J. G. Baer, Neuchatel) that Monard did not designate any type specimens or leave behind any harpacticoid material at his death. For these reasons, also, I have thought it advisable to exclude *C. carthaginiensis* Monard entirely, pending rediscovery and redescription.

TABLE I
DIFFERENCES BETWEEN *C. spinulipes* POR (1967) AND *C. millerorum* NOV. SP.

Character	<i>C. spinulipes</i>	<i>C. millerorum</i>
Setae on mandibular palp	6	5
P1exp3, setae	3(?injury)	4
P2-P4, exp2 inner seta	not quite to end of exp3	nearly twice as far as end of exp3
♀P5benp, inner seta	setiform and high up the inner edge	spiniform and on a level with the two setiform setae
♀P5exp	about 3 times as long as benp	about 6 times as long as benp

The *C. tenuipes* of Klie (1950, fig. 139) is apparently *C. pusillus* (cf. Por, 1959, fig. 16); in both, the male P5 has four exopodal setae (of which the inner terminal is longer than the outer terminal) and no setae on the basiendopod. However, in Klie's figure the exopod of the male P5 is much longer than in Por's, and the setae on it are much less crowded together. The male P5 of the real *tenuipes* is shown by Bodin (1970, pl. 27).

In such a closely-knit genus as this, one should constantly be on the lookout for further characters which might be useful taxonomically or systematically, and four such possible characters will now be considered.

TABLE 2
OCCURRENCES OF CERTAIN CHARACTERS IN VARIOUS *Cletodes* spp., ACCORDING TO THE AUTHORS CITED

	Sars (1911)	Sars (1920)	Lang (1948)	Por (1959)	Por (1964)	Soyer (1964)	Lang (1965)	Drzycimski (1967)	Por (1967)	Bodin (1970)	Coull (1971)	Present paper
<i>tenuipes</i>	-?a		b	+bcd						+e		
<i>limicola</i>	-c		cd		+c					+d		
<i>longicaudatus</i>	-cd		cd			-b						
<i>pusillus</i>		-ab	ab									
<i>longifurca</i>			+c									
<i>reyssi</i>						+bc						
<i>hartmanae</i>							+b					
<i>latirostris</i>								+e				
<i>yotabis</i>									+a			
<i>spinulipes</i>									+bc			
<i>smirnovi</i>										+d		
<i>pseudodissimilis</i>											+b	
<i>millerorum</i>												+c

Key to table: + or -, presence or absence of opercular sensillae; a to e, nature of opercular margin. a = smooth, no spinules or setules; b = smooth, with tiny spinules or setules let into the margin; c = smooth, with discrete teeth let into the margin; d = margin itself cut into small teeth; e = margin itself cut into large teeth.

(1). The sensillae at either end of the operculum have often been figured in the literature (Table 2); it may be wondered whether their apparent absence in the Norwegian material (as in Sars, 1911) of *C. limicola* and *C. tenuipes* is due to an oversight by Sars, or whether it constitutes a genuine difference between the Norwegian population on the one hand and the Black Sea and eastern Mediterranean populations (Por, 1959, 1964a) on the other. Neither Sars nor Soyer (1964) show opercular sensillae for *C. longicaudatus*, so it is possible that this species genuinely lacks them; for *C. pusillus* there are no later figures to confirm or contradict those of Sars, and all the other species in Table 2 are known to have opercular sensillae, placed at the very end of the operculum in all save *C. smirnovi*. The published figures of *C. carthaginiensis*, *C. dissimilis* and *C. pseudodissimilis* are not sufficient to establish either the presence or absence of opercular sensillae, but they are definitely present in a female paratype of *C. pseudodissimilis* which I have examined. The arrangement of the sensillae over the rest of the body is still less well known; *C. hartmanae* is the only species whose figures show this clearly and I very much regret that the type of *C. millerorum* had been dissected before the possible importance of this feature had occurred to me.

Also in Table 2 are included arbitrary categories into which the varieties of opercular margin appear to fall; however, new figures of nearly all known species are required for a realistic appraisal of these characters.

(2). Bodin (1970) shows 'membraneous tubes' on the limbs of several genera, including *Cletodes*, and gives reason for thinking that they have often been mistaken in the past for setae; I have not yet seen them on any harpacticoid, and they are definitely absent from the holotype of *C. millerorum*.

(3). In Table 3, the males of all adequately known species are arranged in three groups, A, B, and C, according to the nature of the second endopod segment of the third swimming-leg in the male (abbreviated as P3enp2); an attempt is made to correlate such modification with the setal formula of the homospecific female. As an example of how the table works, at the end of the generic setal formula at the top it will be seen that the exopod of P5 is given as 5 (i.e. every species of *Cletodes* has five setae on the female P5 exopod), whereas the basiendopod has the letter p. In the column marked p in the table, we find that every species in group A has three setae on the basiendopod, whereas the various species in the other groups may have from one to four basiendopodal setae (the specific number, however, being constant). Thus, in the generic setal formula, numbers denote parts of the formula which are constant at the generic level, and letters parts which are constant only at the specific level.

The only characters showing complete correlation with all three groups are h, j, and n; character p correlates completely with groups A and B, and characters g and l with groups B and C. It is tempting to use these correlations to predict the type of sexual modification in a known male for which this modification has not been described, such as *C. longifurca* Lang; the female of this species agrees perfectly with group B in the 'strong' characters h, j, and n, has only two basiendopod setae on P5 (thus group B or C but not A), and has character g = 1 and character l = 0; the last-named character indicates B rather than C but is neutral as to A, while g is the only character which runs directly counter to the others by indicating C or A rather than B. Thus it seems very

TABLE 3A
GENERIC SETAL FORMULA FOR FEMALE *Cletodes**

P1		P2		P3		P4		P5	
exp	enp	exp	enp	exp	enp	exp	enp	exp	benp
0.0.a	0.b	0.c.4	0.def	0.g.4	0.hij	0.k.4	0.lmn	5	p

TABLE 3B
SPECIFIC SETAL FEATURES FOR SUBSTITUTION IN THE GENERIC FORMULA OF FEMALE *Cletodes*

Group	Male P3enp2	Species	a	b	c	d	e	f	g	h	i	j	k	l	m	n	p
A	unmodified	<i>hartmanae</i>	4	3	0	1	1	0	0	0	1	1	0	0	1	1	3
		<i>limicola</i>	4	3	1	0	2	0	1	0	2	1	1	0	2	1	3
		<i>longicaudatus</i>	4	3	1	0	2	0	1	0	2	1	1	0	2	1	3
		<i>spinulipes</i>	3	3	1	0	2	0	1	0	2	1	1	1	2	1	3
		<i>pseudodissimilis</i>	4	3	1	0	2	0	1	0	2	1	1	1	2	1	3
B	modified one seta	<i>smirnovi</i>	4	2	0	0	2	0	0	0	1	0	1	0	1	0	2
		<i>pulsillus</i>	4	3	1	0	1	0	0	0	2	0	0	0	2	0	2
		<i>tenuipes</i>	4	2	0	0	1	0	0	0	1	0	0	0	1	0	1
C	modified two setae	<i>reyssi</i>	4	3	1	0	2	0	1	1	1	1	1	1	1	1	2
		<i>latirostris</i>	4	3	1	1	2	1	1	1	2	1	1	1	2	1	3
		<i>yotabis</i>	4	3	1	0	2	0	1	1	2	1	1	1	2	1	4

*The letters a to p in table 3A refer to variable features which are further described in Table 3B which lists the species of *Cletodes* in three groups based on the nature of the male P3enp2.

likely that the male of *C. longifurca* will be found to belong to group B; in partial support of this, Lang (1948) says that the third endopod is indeed modified, but neither he nor Por (1964b, the only other find known to me of male *longifurca*) state how many setae it has. The female of *millerorum* has the same setal formula as *pseudodissimilis* (and, except for character a, as *spinulipes*), so the undiscovered male of *millerorum* will probably be found to belong in group A.

(4). Though very small and hard to see, the forms and setations of the rami of the maxillule are of potential taxonomic importance. In *longicaudatus*, *longifurcatus*, *pulsillus*, *tenuipes* (all according to Lang, 1948), and *latirostris* (in Drzycimski, 1967), nothing is said about these rami except that (by implication) they both consist of setae arising directly from the basis, without any free segment. *C. pseudodissimilis* also has this kind of endopod (with two setae), and no sign whatever of an exopod. All the other species (*limicola*, *reyssi*, *smirnovi*, *spinulipes*, *millerorum*, *hartmanae*, and *yotabis*) have two setae on the exopod, which in *limicola* has a free segment bearing the setae, according to Lang (1948), but only the two setae unaccompanied by any free segment according to Soyer

(1964). As to the endopod, only *millerorum* has a free segment, which bears three setae (Fig. 6); in all the other species the endopodal setae, to the number of three (*reyssi*, *smirnovi*, Soyer's *limicola*), two (*hartmanae*, *spinulipes*, Lang's *limicola*), or one (*yotabis*), arise directly from the basis, as in *pseudodissimilis*. At present there appears to be no correlation between any of these characters and the grouping shown in Table 3.

Most species of *Cletodes* appear to be well-founded, but the amount of real or supposed variation in *C. limicola* calls for further investigation. The need to give the clearest possible figures of every feature of every species, whether newly discovered or well known, cannot be too strongly emphasised.

REVISED KEYS TO SPECIES OF *Cletodes*

FEMALES

1. P3exp2 without, P4exp2 with, an inner seta *smirnovi*
 These segments each without an inner seta 2
 These segments each with an inner seta 4
2. P2exp2 with an inner seta; P2–P4, enp2 with 1, 2, and 2 setae respectively;
 P5benp with 2 setae; furca long and slender *pusillus*
 P2exp2 without an inner seta; remaining characters not combined 3
3. P3–P4, enp2 with 1 seta each; P5benp with 1 seta; furca slender, slightly
 bent at the base *tenuipes*
 P3–P4, enp2 with 2 setae each; P5benp with 3 setae; furca elongate oval
 *hartmanae*
4. P2enp2 with 4 setae *latirostris*
 P2enp2 with 2 setae 5
5. P3enp2 with 3 setae, P4enp2 with 3 or 4 setae 6
 These segments each with 2 setae *longifurca*
 These segments each with 4 setae *yotabis*
6. Furcal rami irregularly shaped *dissimilis*
 Furcal rami broadest near the base, with or without a basal expansion, but
 in either case tapering more or less evenly towards the apex 7
7. Furca about 7 times as long as broad; P5benp with 2 setae *reyssi*
 Furca about 5 times as long as broad; P5benp with 3 setae *longicaudatus*
 Furca between 2 and 3 times as long as broad; P5benp with 3 setae 8
8. P5 rami fused(?) *carthaginiensis*
 P5 rami discrete 9
9. P1exp3 with 3 setae *spinulipes*
 P1exp3 with 4 setae 10

10. P4enp2 with 3 setae *limicola*
 P4enp2 with 4 setae 11
11. Furcal ramus markedly bulging outwards, short and pear-shaped; P4exp3
 outer marginal spines, upper much shorter than lower . *pseudodissimilis*
 Furcal ramus not bulging outwards, moderately slender and tapering evenly;
 P4exp3, the two outer marginal spines subequal . *millerorum*

MALES

1. P3 not modified, but resembles that of the female (group A in Table 3) . 6
 P3enp2 with a terminal hook-like thorn, and one or two setae . 2
2. P3enp2 with 1 terminal seta (group B) 3
 P3enp2 with 2 terminal setae (group C) 5
3. P4exp2 with an inner seta; P5exp with 3 setae . . . *smirnovi*
 P4exp2 without an inner seta; P5exp with 2 or 4 setae . . . 4
4. P5exp with 2 setae; P2exp2 with an inner seta . . . *pusillus*
 P5exp with 4 setae; P2exp2 without an inner seta . . . *tenuipes*
5. P5exp with 5 setae; P2enp2 with 2 setae; P3enp2 with a very long outer
 terminal seta and a short inner terminal seta . . . *reyssi*
 P5exp with 5 setae; P2enp2 with 4 setae; P3enp2 with 2 terminal setae of
 about the same length . . . *latirostris*
 P5exp with 3 setae; P2enp2 with 2 setae; P3enp2 as in *latirostris* . *yotabis*
6. P5, exp with 2 large terminal setae and a small outer seta, benp with no setae
 at all; furca at most twice as long as broad, and usually less; P3-P4, exp2
 without an inner seta . . . *hartmanae*
 P5 variable; furca at least twice as long as broad; P3-P4, exp2 with an
 inner seta 7
7. P5exp with 2 setae (benp with 1 seta); furca about 5 times as long as broad
 . . . *longicaudatus*
 P5exp with 3 setae; furca less than 4 times as long as broad . . . 8
8. P5benp with a seta *limicola*
 P5benp without a seta 9
9. Furcal rami broadest near the base, tapering evenly; P5exp outermost seta
 small (as in *hartmanae*) . . . *spinulipes*
 Furcal rami irregular in form; P5exp outermost seta stout and spiniform
 . . . *pseudodissimilis*

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AN IRISH MIDDLE BRONZE AGE SPEARHEAD IN THE QUEENSLAND
MUSEUM, BRISBANE

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Amongst the small quantity of Old World antiquities in the Queensland Museum, is a cast bronze spearhead, registered H42 (previously A4164), length 18.6 cm, here illustrated in Plate 31; its provenance is recorded simply as Ireland and in the museum register it is described as a 'Roman spearhead'. The spear, the gift of a Mrs O'Doherty, is registered as having been donated on 16 January 1884; no further details are known as to the circumstances of its discovery. The angular or 'kite-shaped' blade and the twin flattened loops, lozenge shaped in plan and placed low down on the tubular socket, probably decorative rather than functional, in fact readily identify this spearhead as a type commonly assigned to the earlier part of the Middle Bronze Age in Ireland where some 400 examples are known (Mitchell, O'Leary and Raftery, 1941, pp. 288–92 esp. fig. 1; Eogan, 1962, pp. 45–6; 1964, pp. 268–9). These spears were cast in two-piece moulds as can be seen from the partially cleaned down flashing or casting seams still visible either side of the socket of the Queensland Museum spearhead. A scattering of kite-shaped spearheads—which have a number of variants marked mainly by the nature, presence or absence, of the central raised ribs on the blade and socket—extends the distribution to Scotland (Coles, 1963–64, pp. 104–56) and Southern England (Smith, 1959, pp. 179–80).

First classified by Greenwell and Brewis (1909, p. 459) as Class III of their typology of British Bronze Age spearheads, these are Class C of Coles's more refined scheme and Group I of Britton's recent typological and technological study of examples in the Pitt-Rivers Museum, Oxford (Allen, Britton and Coghlan, 1970, p. 156). Precise dating of kite-shaped spearheads is not easy since, despite their usual ascription to the Middle Bronze Age (on conventional dating, from 1400 B.C.), the few associated finds contain only Late Bronze Age material (dated to after 900 B.C.). A number of two-piece stone moulds used in the production of Group I spearheads—all from Ireland—have also been used for casting typical and well-dated Middle Bronze Age objects such as dirks and rapiers. Some additional support for the presumed early date of many Group I spearheads is given by their morphological relationship to Early Bronze Age tanged forms.

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A number of spears similar to the Brisbane example have been subjected to metallurgical analysis (Brown and Blin-Stoyle, 1959a, b; Allen, Britton and Coghlan, 1970, nos. 73-8). Of these a selection from spearheads of Irish provenance may be compared with the results of chemical and spectrographic analysis by the atomic absorption method obtained, as on previous occasions, through the good offices of the Commonwealth Defence Standards Laboratory (Megaw, 1969).

It will be seen from a comparison of the analysis of the Brisbane spearhead with others cited in Table I that it shares with them the characteristic features of a typical tin-bronze alloy with few significant trace elements which may include arsenic, arsenical copper being much in use for the manufacture of early Irish bronzes (Coghlan and Case, 1957, pp. 98-9). Low antimony and bismuth is a key feature of many Middle Bronze Age

TABLE I
CHEMICAL AND SPECTROGRAPHIC ANALYSES OF IRISH GROUP I SPEARHEADS

Specimen	Cu%	Sn%	Pb%	As%	Sb%	Ag%	Ni%	Bi%	Fe%	Hardness*
Queensland Museum H42	85.8	12.3	0.002	n.d.	n.d.	0.02-0.05	n.d.	n.d.	0.2	ca. 100
ABC no. 73 BBS no. 356	86.3	5.268	<0.02	n.d.	<0.05	0.029	<0.01	<0.005	0.0069	85.3
ABC no. 75 BBS no. 351	92.0	7.6	<0.02	n.d.	n.d.	0.34	n.d.	<0.005	0.046	68-104
ABC no. 76 BBS no. 349	88.0	10.60	0.04	0.74	<0.05	0.31	0.18	<0.005	0.012	
BBS no. 54	87.7	10.4	0.73	0.71	<0.05	0.046	0.29	<0.005	0.011	
BBS no. 55	89.0	10.5	0.04	0.24	n.d.	0.005	0.069	<0.005	0.0082	
BBS no. 60	88.2	10.0	0.97	0.58	<0.05	0.027	0.20	<0.005	0.0088	
BBS no. 61	86.8	13.0	0.03	n.d.	n.d.	0.016	0.013	<0.005	0.043	
BBS no. 62	82.5	17.3	<0.02	n.d.	<0.05	0.036	<0.01	<0.005	<0.006	
BBS no. 93	86.1	12.0	0.68	0.89	<0.05	0.040	0.33	<0.005	0.040	
BBS no. 94	83.8	15.1	1.13	0.82	<0.05	0.036	0.31	<0.005	0.010	
BBS no. 95	91.0	8.9	<0.02	n.d.	<0.05	<0.005	0.014	<0.005	<0.006	
BBS no. 348	85.6	14.1	<0.02	n.d.	n.d.	0.21	n.d.	<0.005	0.064	

ABC = Allen, Britton and Coghlan, 1970; BBS = Brown and Blin-Stoyle, 1959a, b; n.d. = not detected.

* For specimen H42 hardness is expressed on the Vickers scale, for all other specimens in equivalent Brinell Units.

pieces. The hardness figures are consistent with general evidence for some considerable degree of cold work hardening of at least the cutting edges.* As however has been recently observed (Allen, Britton and Coghlan, 1970, pp. 21–2), the average standard of metal represented by these and similar spearheads is not as high as that obtained in the production of other simpler to cast objects of Middle Bronze Age date.

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* Owing to the thickness of the surface oxides on the Queensland Museum spearhead the hardness reading was taken on the butt.

PLATE 31

Irish Middle Bronze Age spearhead—Queensland Museum No. H42 (previously A4164).

Scale in cm.







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